

The Kinaesthetic Fusion Effect: Mechanisms and Extensions

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Keywords

Sensory integration, touch, tactile, crossmodal, visual occlusion, proprioception, tactile acuity, intersensory

Abstract

This study investigated the Kinaesthetic Fusion Effect (KFE) that was first described by Craske and Kenny in 1981. It was reported that when, without vision, participants pressed a button that resulted in a probe simultaneously touching the contralateral limb at a displaced location, they perceived an apparent change in limb length.

The current study did not fully replicate these earlier findings. Participants did not perceive any reduction in the sagittal separation of the button and probe following repeated exposure to the tactile stimuli that was present on both arms. However, a localised and partial medio-lateral fusion was observed, with the touched positions seeming closer together. In addition, tactile acuity was found to decrease progressively for distal positions of the upper limb and a foreshortening effect was found which may result from a line-of-sight judgment and represent a feature of the reporting method used.

A number of years have elapsed since the description of the original KFE. Although frequently cited in the literature, there has been no further investigation into the mechanisms of action. The results of the current study are considered in light of more recent literature concerning intersensory integration. Future research should focus on further clarification for the specific conditions that must be present for a fusion effect to occur. Finally, this thesis will benefit future studies that require participants to report the perceived locations of the unseen limbs.

Table of Contents

Keywords	2
Abstract	3
Table of Contents	5
List of Figures	7
List of Tables	9
List of appendices.....	10
List of Abbreviations	11
Acknowledgments	12

Introduction.....	13
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LITERATURE REVIEW

Background.....	15
Central Sensorimotor Control.....	16
Overview of Peripheral Sense Organs.....	17
Limb Position sense.....	18
Considerations when testing position sense	20
Sensory System Integration.....	21
Body Schema/Body Image: The internal representation of body awareness for perception and action.....	24
Sensory Systems in Conflict and Related Experiments	25
Sensory Conflict in Studies of Touch and Proprioception.....	27

Principles of multimodal interaction and conflict resolution.....	30
Phantom sensation (The funneling illusion).....	34
Research problems.....	36
Research Aims and Objectives.....	48

MANUSCRIPT

Methods.....	49
Results.....	71
Discussion.....	87
Conclusions.....	107
References.....	108
Appendix.....	128

List of Figures

- Figure 2: The kinaesthetic fusion device
- Figure 3a: Potential results: a localised length change takes place at the right finger section that is perceived to move closer to the body
- Figure 3b: Potential results: a localised length change takes place where the probe makes contact that is perceived to move closer to the body
- Figure 4: A participant sitting in the apparatus, with a cloth draped around the neck to prevent vision of the arms
- Figure 5: A section of the Grid above the arms used by participants to estimate the perceived touched position
- Figure 6: Hands positioned into wedge shaped foam support
- Figure 7: The solenoid probe device sat between the arms
- Figure 8: An example of the participant in position wearing headphones
- Figure 9: Experimental Design
- Figure 10: Approximate five markings for the right arm
- Figure 11: A two dimensional representation of the five actual and reported touched positions for the left and right limbs.
- Figure 12: Constant error during the baseline condition for reported position (sagittal plane)
- Figure 13: The “foreshortening” effect (sagittal plane)
- Figure 14: Transformed line of sight and reported positions for the left and right arms (sagittal plane)
- Figure 15: A frontal view of the foreshortening effect (medio-lateral plane)

- Figure 16: Transformed line of sight and reported positions for the left and right arms (medio-lateral plane)
- Figure 17: Perceived position of the button and probe during the 12.7cm displaced probe condition
- Figure 18: Perceived position for 0% of arm length for the left and right arms and the 12.7cm displaced position for the left arm over the conditions
- Figure 19: Variable error (mean standard deviation) during the baseline condition for the five positions on left and right arms
- Figure 20: Variable error for left and right arms during the baseline condition

List of Tables

Table 1: Craske, Kenny, Keith, 1984 Citations

Table 2: Mean perceived position during passive probed condition for the three conditions for right and left arms. Standard deviation in parentheses

List of appendices

- | | |
|-------------|-------------------------------|
| Appendix 1: | Ethics approval |
| Appendix 2: | Participant recruitment flyer |
| Appendix 3: | Participant consent form |

List of Abbreviations

KFE – Kinaesthetic Fusion Effect

fMRI – Functional Magnetic Resonance Imaging

CNS – Central Nervous System

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The Kinaesthetic Fusion Effect: Mechanisms and Extensions

Introduction

Craske and Kenny first illustrated the Kinaesthetic Fusion Effect (KFE) in 1981. This effect describes the way in which a touching action made by the index finger is experimentally displaced between a button and solenoid probe to a position 12.7cm closer to the body on the parallel, contralateral arm. This action results in a sensory discrepancy that is soon recalibrated so that the individual perceives there to be no spatial discrepancy. A follow-up study by the same authors in 1984 clarified the effect, whereby it was suggested that the adaptation was a result of the participant perceiving the arm length to increase for the probed arm and decrease in length for the arm which was involved in pressing the button. The KFE is an example of an adaptation phenomenon in human perception, and is one of only a few that involves the sense of touch.

This research can lead to a greater understanding of sensory integration between touch and proprioception. A number of studies have cited the KFE within the field of study of body representation (Bianchi, Ivana, Savardi, Ugo, Bertamini, Marco, 2008; Ehrsson, Holmes, Passingham, 2005; McDonnell, Scott, Dickison, Theriault, Wood, 1989), but to date, no replication or extension of those previous findings has been undertaken. Therefore, the purpose of the current thesis is to answer a series of problems that need to be resolved, including: replicating the findings of Craske et.al (1984) to determine if the KFE results in a perceived length or position change of the limbs; to investigate if a similar fusion occurs whereby the limb separation in the

medio-lateral plane is perceived to be reduced; to improve the existing methodology; and finally to outline tactile/proprioceptive acuity and bias for various positions on the arm, hand and finger during visual occlusion. These problems have been identified to provide a greater understanding of the KFE.

Literature Review

Background

This thesis will present an experiment designed to achieve a greater understanding of the Kinaesthetic Fusion Effect (KFE), a phenomenon first described by Craske and Kenny in 1981.

In order to explain the rationale for the proposed experiment, a review of the literature will outline relevant findings from related research in sensorimotor perception, which are linked to KFE. The first section will detail some theories relating to how the sensorimotor system processes diverse sensory information to plan movements. In the second, the neurophysiological processes that lead to perception of touch and proprioception, each in isolation, will be briefly reviewed. In addition, this section will consider evidence from selected neuroimaging and movement studies, and research on patients with brain damage to highlight the capacity for integration of sensory information. In the third section, a selection of experiments in which sensory information has been manipulated will be described. These experiments explore the diverse adaptations that can take place due to discordant sensory signals between two sensory modalities. Finally, specific research germane to this thesis involving sensory discordance and the resulting adaptation involving touch and proprioception will be provided and questions that remain unanswered about the process of the KFE will be presented.

Central Sensorimotor Control

Human motor control involves a series of feedforward and feedback information loops (Schmidt & Lee, 1995). The brain can be thought of as holding an internal representation of the body (a body schema). In this schema, the desired movements (feedforward) are coordinated with sensory feedback related to the action. Receptors of touch, vision, proprioception, smell, sound and balance can work in isolation. Alternatively, these receptors may be combined to provide the individual with a coherent perceptual view of their immediate environment. Occasionally, however, information delivered from the environment to the receptors can be misleading, such as when two sensory systems provide different information about the same event. Although this action may cause a problem initially, the normally functioning brain can adapt and adjust to such distortions. Bastian (2008) defines sensorimotor adaptation as the trial-and-error progression of regulating movement to new sensory demands. The adaptation results in a perceptual adjustment, where the outcome depends on the nature of the setting and the sensory conflict. When the brain is confronted with the challenge of reconciling discordant sensory information, its adaptability is usually very efficient (O'Dwyer, 1996). For instance, the perception of stimuli or an event can be altered when conflicting information arises – such as hearing a voice in one spatial location and seeing moving lips in another, leading to the perception that the sound is coming from the visual stimulus (the Ventriloquist Illusion). The brain can also compensate for the discrepancy by adapting the individual's behaviour in order to match motor control to the environment perceived. These error-driven adaptations may be essential for accurate perceptual motor coordination (Craske et.al, 1984). Neuroplasticity studies have provided empirical

evidence to support the idea of neural flexibility and malleability in the central nervous system (Pons, Garraghty, Ommaya, Kaas, Taub & Mishkin, 1991), and this is an important feature for the effective functioning of the sensorimotor system (Sanes & Donoghue, 2000).

Overview of Peripheral Sense Organs

Touch

Discriminative touch is the perception of pressure, vibration, and texture (Shepherd, 1994) and is mediated by specialised receptors. Discriminative touch relies on four different receptors in the skin: Meissner's corpuscles, Pacinian corpuscles, Merkel's disks, and Ruffini endings (Shepherd, 1994). The first two are considered to adapt rapidly as firing stops quickly in response to a constant touch stimulus. The second two are considered to adapt slowly because firing does not stop during discriminative touch. The receptors connect to sensory axons or primary afferent axons. The axons then ascend in the dorsal white matter of the spinal cord to the brain.

Proprioception

Proprioception provides a sense of the position of our body parts and their movements. The terms proprioception and kinaesthesia have come to be used interchangeably, although it should be noted that proprioception has been considered the sense of position, whereas kinaesthesia is associated with the sense of movement (Stillman, 2002). Proprioceptive sensation relies on receptors in muscles, joints and skin (Shepherd, 1994). The muscle spindle is the major stretch receptor within muscles and delivers muscle length and velocity information. Golgi tendon organs and joint afferents also monitor stresses and forces at the tendons and joints. The

proprioceptive system arises from the afferents entering the spinal cord or via the cranial nerves. These are the afferents from muscle spindles, Golgi tendon organs, and joint receptors. Skin receptors have also been shown to participate in the sense of proprioception (Edin & Johansson, 1995). The axons travel with the discriminative touch system before diverging to the separate areas of the brain. Although not a direct focus for the present investigation, it is worth mentioning that lesions to the thalamus critically disrupt proprioceptive sensibility (McCloskey, 1978), whereas the primary somatosensory cortex and cerebellum can process both tactile and proprioceptive information, independent of each other.

Limb Position Sense

Many years of research utilising a variety of methods have allowed scientists to understand the mechanisms that lead to the perception of position sense. Early work by Gross, Ross, Melzack (1974) proposed that spatial localisation of body positions and parts is dependent on peripheral sensory input, efferent output and central organisation of these signals. Although joint receptors were once thought to contribute significantly to position sense, this position was modified following demonstrations that those joint receptors that participate in position sense are only active at extreme positions (Clark, Burgess, 1975). The main source of proprioception appears to come from the muscle spindle. Evidence for this was provided when removal of skin and joint receptors minimally reduced position sense (Ferrell and Craske, 1992). Position sense can also be altered, causing illusions of movement, by applying vibration to the muscle spindles (Lackner, DiZio, 2002). Specifically, when the participant cannot see their arm, a perceived stretch of the muscle is induced so that, for example, were the biceps brachii to be vibrated this would cause the perception that the elbow is

extending. Interestingly when a participant is asked to close their eyes and hold their nose while the biceps is vibrated a 'Pinocchio illusion' results, whereby the person believes that their nose is lengthening in the same direction of elbow extension (Lackner, DiZio, 2002).

Without the availability of proprioception, an individual with peripheral neuropathy is largely unaware of the position of their body unless vision constantly monitors the limbs (Cole, 1981). Limitations of proprioceptive signals have been identified where feedback from movements is thought to be delayed by between 80ms and 250ms (Paillard 1999; van Beers, Haggard, Wolpert, 2004), and therefore cannot influence corrections to very fast movements which are planned using a feedforward mechanism.

Proprioceptive drift

In healthy individuals, limb position sense drifts when vision of the limb is not available. This drift occurs towards the participant's body and increases over time, Wann and Ibrahim (1992). One view of this phenomenon proposed by Jeannerod, (1989) is that the internal representation updated by the sensory interaction of vision and proprioception requires constant moderation and recalibration and when the central controller is deprived of this detail, the internal model drifts over time. The study by Wann et.al, 1992, also ascertained that drift can be halted with brief glimpses of the limb position or when the participant was asked to isometrically contract the limb.

Several other factors influencing limb position sense have been identified and include age (Kaplan, Nixon, Reitz, Rindfleish, 1985); efference copy or motor commands (Gandevia, Smith, Crawford, Proske, Taylor, 2006); fatigue (Allen, Proske, 2006); head and neck position (Knox, Hodges, 2005); active and passive movements (Paillard, Brouchon, 1968; Boyle and Negus 1998); muscle contraction history (Walsh, Smith, Gandevia, Taylor, 2009); space and tasks (Fuentes, Bastian, 2010); intersensory conflict between vision, touch and proprioception (Botvinick, Cohen, 1998); gravity cues (McCall, Goulet, Boorman, Roy, Edgerton. 2003); and ischemic block (Gross, Melzack, 1978). During an experiment in which participants were deprived of vision of their arm, it was found that judgements of the position of the arm were closer to the midline than reality and closer to the body (Gross, Ross, Melzack, 1974). Limb position sense is also affected in specific populations, such as those afflicted by Parkinson's disease (Zia, Cody, O'Boyle, 2000), as well as ballet dancers and highly trained gymnasts (Lephart, Giraldo, Borsa, Fu. 1996; Ramsay and Riddoch 2001). A number of studies have investigated if gender affects positional sense; however, no differences have been found. (Koralewicz, Engh, 2000)

Considerations when testing position sense

Many considerations need to be assessed when measuring position sense. Several studies have involved participants pointing, or position matching of the perceived position with the contralateral limb. This method has raised questions about the extent to which proprioception alone is measured. Pointing may result in additional variability in responses due to inter-hemispheric transfer of information as well as motor output variability (Wilson, Wong, Gribble, 2010). The experiment presented in

this thesis could not use a pointing task due to the requirement of the experiment to conceal both upper limbs. In Craske et.al (1984), participants pressed a button with the right index finger that activated a solenoid probe that was displaced 12.7cm closer to the body, causing it to touch the left arm. The subject then was asked to indicate the sagittal separation of tactile stimuli by an approximation in length (in inches). This could raise many threats to internal validity whereby large variations between subjects could influence results. Since 1984, a number of experiments have introduced methodology to measure perceived position of a limb without the task of pointing (Wilson et.al, 2010; Jones, Cressman, Henriques, 2010). Furthermore, usually a blindfold is worn during proprioceptive testing to prevent visual cues (Callaghan, Selfe, Bagley, Oldham. 2002), or alternatively, participants close their eyes (Bodegård, Geyer, Herath, Grefkes, Zilles, Roland, 2003). Some authors aimed to reduce auditory cues during limb position testing by playing music or white noise through headphones (Chu, Kane, Arnold, Gansneder, 2002). The sense of proprioception itself does not reveal auditory cues but any equipment used may reveal relevant location cues for the participant (Carpenter, Blasier, Pellizzon, 1998).

Sensory System Integration

It is well established that the different regions of the brain function in an efficiently organised system (Duchaine, Cosmides & Tooby, 2001). Therefore, sensory input from the environment is unlikely to involve processing in only one individual sensory channel to generate perception. Development of interactions between the sensory systems appears to be structured so that if there is deprivation of information in one modality, another reliable source is available. For example, when one searches for keys in the dark, the interaction of touch and the sound of the keys with active

movement delivers an accurate representation of the keys and their location, and some of its properties (a capacity known as stereognosis), and will provide the individual with richer information than if they had only touch to rely on.

Evidence from imaging and electrophysiological studies of proprioception, touch and vision integration

More recently, researchers have been able use various high resolution imaging devices, such as functional Magnetic Resonance Imaging (fMRI), to record brain activity for bimodal tasks. A study conducted by Kavounoudias, Roll, Anton, Nazarian, Roth & Roll (2008) set out to explore how proprioceptive and tactile messages can produce a cohesive percept of an individual's movement. For instance, by producing kinaesthetic illusions from touch and proprioception stimuli, it was possible to identify areas of related brain activation. Of particular importance were the areas involved in spatial and temporal processing of the multisensory information, which has been described for sensory integration by Spence, Sanabria & Soto-Faraco (2007). The results show that the inferior parietal lobule and the insula were highly activated. These areas are known to become active during crossmodal processing for object movement within areas in reach or in the peripersonal space (Bremner, Schlack, Duhamel, Graf & Fink, 2001) and during various cognitive tasks, if sensory integration occurs concurrently (Olson, Gatenby & Gore, 2002). This study not only outlines the areas of the brain involved in processing sensory information but also provides an example of sensory convergence underpinning human perception. Furthermore, Bernier, Burle, Vidal, Hasbroucq and Blouin, 2009, collected median nerve somatosensory evoked potential data during a novel visuomotor mirror tracing

task. It was found that the proprioceptive signals were suppressed to enable adaptation to the sensory conflict between vision and proprioception.

Improved movement control during sensory system integration

Crossmodal integration of sensory information is vital for a precise perception of an individual's environment, and is essential for accurate motor coordination, so that movement can be corrected. This ability has been reported in cases where visual feedback is temporally or spatially delayed in reaching movements (Pratt & Abrams, 1996). A correction of the reaching movement in relation to the delay still occurs even if the change in visual feedback has not been explicitly perceived (Goodale, Pelisson & Prablanc, 1986), and therefore suggests sensorimotor integration can involve unconscious processing. Proprioceptive information has also been shown to improve smooth pursuit eye movement. For example, ocular pursuit of a moving target is improved when target movement is concurrently monitored manually (Gauthier, Vercher, Mussa Ivaldi & Marchetti 1988). Similarly, concurrent manual tracking of a moving visual stimulus can benefit judgments about the target's future position (Tanaka, Worringham, Kerr, 2009). These examples highlight the importance of the control of movement through separate and converging sensory information.

Body Schema/Body Image: The internal representation of body awareness for perception and action

Penfield (1950) empirically demonstrated the existence of brain maps on the cortex related to sensory information from the body surface and corresponding motor regions. These brain areas are roughly proportional in size to the number of receptors or axons for that region. Numerous neurophysiological and neuropsychological studies suggest that this information is integrated and processed further at a higher level to create a cognitive model of the body (Gallagher, 2005). This model has been divided further into the body image and body schema. The body image is defined as a visual representation of the body from an outside perspective or top-down view. A study by Reitman and Cleveland (1964) induced changes in the body image as a result of sensory deprivation, and suggests sensory signals play a part in constructing this internal model. By contrast, the body schema describes the internal spatial representation of the body segments, which is revised following movement. Head and Holmes, (1912) suggested that the body schema is a “plastic continually changing standard”. Disorders of the body schema have been used to explain why some individuals are unable to avoid obstacles while walking (Kephart, 1960). When patients with brain damage have been studied, findings have led scientists to dissociate these two internal models and conclude that the body schema does not penetrate conscious awareness, and is utilised during voluntary action. The body image, on the other hand, is consciously accessed by the individual, as illustrated by participant reports from a sensory deprivation study conducted by Reitman et.al (1964). The investigators noted that their participants believed that

"their arms seemed to be dissociated from their body; their body seemed to become smaller, they had sensations of floating in air".

These two representations have been applied to interpret changes that take place in perception and action following sensory conflict (Kammers, Mulder, de Vignemont, Dijkerman, 2009) and provide a framework for updating body awareness and position.

Sensory Systems in Conflict and Related Experiments

One tool used in multisensory integration research is the experimental conflict situation. This occurs when two modalities receive incongruent signals from their respective receptors regarding a single aspect of the environment, generally resulting in greater adaptation or illusion in one modality than the other. Introducing this experimental manipulation permits a greater understanding of the processes that recalibrate the senses. Research studies in prism adaptation, for example, von Helmholtz (1926) and the rubber hand illusion, and Botvinick & Cohen (1998), have demonstrated changes in perceptual alignment if conflicting sensory information needs to be resolved. The prism adaptation effect has been cited in a large number of enquiries within crossmodal integration of vision and proprioception. Many variations of the experimental design exist. However, generally the manipulation involves a person wearing wedge prisms that laterally displace the visual field to the right or left. The subject subsequently produces motor output, for example, pointing to visual targets, and is provided with feedback about those movements from other sensory systems. To begin with, the individual makes pointing errors to the right or left of a target, depending on the displacement by the prisms. Vision and proprioception provides feedback to the individual that their current percept of the environment is inaccurate. Subsequently the next motor plan is altered to incorporate the previous

feedback. After this practice, these errors can decrease towards zero over the course of as few as ten pointing trials (Martin, Keating, Goodkin, Bastian, Thach, 1996).

The rubber hand illusion differs in that it does not involve motor output to cause a perceptual change. The spatial and temporal sensory information is important for the perceived shift in hand position (Costantini, Haggard, 2007). The setup involves the experimenter stroking a person's hidden finger and hand, and synchronously stroking an observable rubber hand. A typical finding is that the individual has the sensation that the rubber hand is a part of their body and feels the touch of the stroke (Botvinick et.al, 1998).

These two studies serve to illustrate that the perception of the body schema or image has changed to preserve a coherent overall interpretation of sensory input and motor output. In the prism experiment, movement error feedback from proprioception and vision create the adaptation (Welch, Warren, 1980), whereas the rubber hand illusion results from the correlated sensory processing of touch and vision. These findings highlight the separate mechanisms underlying perceptual changes. These two processes have been classified as 'adaptation' and 'illusion' (O'Callaghan, Nudds, 2009). For example, during the prism experiment a hallmark of adaptation is that once the experimental manipulation is discontinued an after-effect is observed whereby the individual still executes motor output as in the adapted state when the distortion was present. Pre-exposure function resumes after sufficient movement corrections have taken place. On the other hand, the rubber hand illusion disappears as soon as the stimuli are removed, which suggests a separate processing of sensory information has taken place.

These examples have illustrated that perception and motor output can be altered by sensory conflict independent of each other. Therefore, an illusion can take place when the individual is not required to interact with the environment, but when the individual does interact, adaptive changes occur to both perceptual and motor systems. Although the processes of prism adaptation and the rubber hand illusion may differ, these two examples may reflect the ability for the perceptual and sensorimotor systems to induce a new internal model of the environment. The perceptual changes take place after the sensory signals are processed and relevant inferences are made about the position of the body in space. Extending these ideas, during prism adaptation matching motor output with its resulting sensory feedback suggests a close connection between afferent and efferent signals for movement adaptation. It is also evident that a requirement for perceptual change of body awareness to take place for both of the aforementioned phenomena is synchronous spatial and temporal sensory input.

Sensory Conflict in Studies of Touch and Proprioception

It is important to note that most studies in crossmodal integration and sensory conflict have been undertaken using visual, auditory and tactile inputs. However, this thesis is concerned with the crossmodal integration of touch and proprioception, an area in which there are significantly fewer papers. Ehrsson, Holmes & Passingham (2005), who investigated neural activity using fMRI of the brain during the rubber hand illusion, reported one study. The study findings indicated that blindfolding the individual and directing them to stroke a rubber hand while having their hand stroked synchronously by the experimenter caused an illusion that the participant was stroking their own hand. Consequently, this action induced a perceived shift in body position,

and therefore demonstrated that this perceptual change can occur in the absence of vision.

Kinaesthetic Fusion Effect

A more focused investigation of this area of research was a series of experiments involving discordant information between touch and proprioception undertaken by Kenny & Craske, initially reported in 1981. Study results described an adaptation that took place after the perception of a spatial difference between two spatially separate points of contact on the skin of the base of the left hand and the right index finger. During the KFE, the subject extended both arms out front of the body. Without vision of the arms, the right index finger would flex 90 degrees and push a button (the kinaesthetic fusion device) that was located medially on a plexiglass plate that separated both arms from each other (Figure 1).

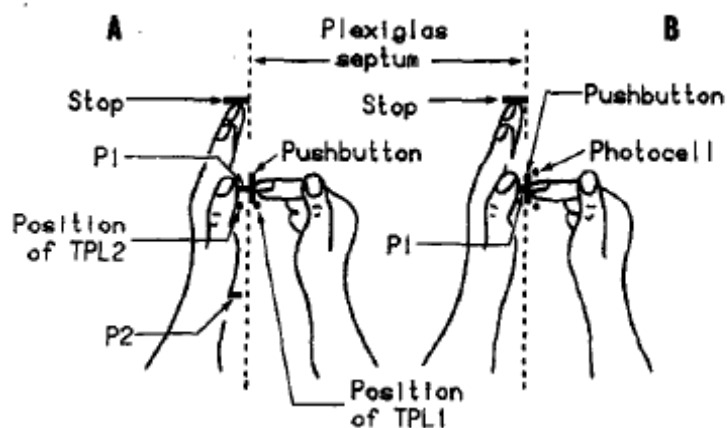


Figure 2: The kinaesthetic fusion device (taken from Craske et.al, 1981)

During the control conditions (0cm probe displacement condition), a probe would touch the middle of the left palm, resulting in no felt discordance between limbs.

However, during the experimental condition, instead of the probe touching the middle

of the left palm, it was displaced 12.7cm (12.7cm probe displacement condition) closer to the body than the 0cm probe displacement. A sensory difference was felt at first between the two positions being touched, but soon recalibrated, after 15 to 20 trials, so that the individual reported the difference to be zero, creating the KFE. A delay of four seconds was also introduced after the onset of pushing the button and the felt probe. This still produced a discrepancy between stimuli and a resulting fusion of the positions. When the subject was returned to the original control condition an after-effect similar to that in prism adaptation occurred wherein the probe, which was now directly opposite the button, was felt to be further away. Although these results show a clear effect, the distance between the probe and the right finger was estimated by the subjects and reported verbally in inches; inconsistent knowledge between subjects and within subjects of how long an inch is may have reduced the accuracy of the reported positions. The authors ran another two experiments and found that index finger joint adaptation or postural after-effects (a change in perceived shoulder angle from the horizontal could be the cause of the fusion) could not explain the results.

Pursuing the Kinaesthetic Fusion Effect

In a follow up study published in 1984, Craske & Kenny investigated the phenomenon of intersensory integration causing the KFE. The extent of adaptation for both arms was explored by a visual/tactile crossmodal judgment made by placing a microlight above the veridical location of the subject's left and right fingertip. By introducing this manipulation, it was found that the touch on one arm (left) was perceived to be further away from the body than the light and closer than the light on the opposite (right) arm. The introduction of vision caused crossmodal integration of proprioception and vision. A reduction in the perceived sensory difference between

the light and the touched area when the visual stimulus was introduced, was attributed to the light cueing vision to recalibrate the participant's perception, and was more powerful than the tactile/proprioceptive treatment. The authors suggested that adaptation took the form of a change in perceived limb length, because after-effects that were large at the fingertip and wrist vanished to zero when an area on the right forearm (which was further away from the probed area) was touched. This was aimed to signify that a perceived position change could not have provided the impetus for the illusion as all sections of the arm should display after effects. This was shown when the participant was asked to estimate the anterior-posterior difference between a touch and a microlight, which was directly above where the touch took place. Craske et.al (1984) interpreted this as evidence that because the adaptation did not extend to other parts of the arm, perceived change in arm position could not have been the cause. It was also found that passive finger movement still caused adaptation and after-effect; and if the probing arm did not make contact with the button but a resulting probe on the opposite arm still occurred, a fusion did not result. It should be noted that a minority of participants reported no fusion effect and therefore this finding should be taken into consideration. Prior sensory conflict adaptation research shows the site of storage for adaptation representation is the cerebellum, and is likely to be similar for this context (Lang & Bastian, 1999).

Principles of multimodal interaction and conflict resolution

Why does the brain interpret the separate sensory information as a fusion that results in forfeiting the internal representation of the body? Welch & Warren, 1980, Stein & Meredith, 1993, and O'Callaghan et.al, 2009 provide reviews of multimodal interaction and conflict resolution. The primary findings from these reviews that

share common ground will now be presented. Research suggested that spatial and temporal information is vital during sensory integration. When stimuli presented to separate sensory systems occur in the same space and time, the central nervous system automatically structures this information into one (Bedford, 2001). Bedford (2004) has suggested that this grouping occurs because the internal representation of the world created by the brain is aware that two or more events cannot occupy the same space and time, and that a single event cannot occupy discordant characteristics. Above a threshold, the dominant modality succeeds in altering perception. The dominant modality has been explained by a theory of ‘modality appropriateness’. That is the sensory system that is most appropriate for the particular context, will be weighted more than the other modality. It is accepted that generally vision is the dominant modality for spatial features whereas audition is appropriate for temporal information (Wada, Kitagawa, Noguchi, 2003). Recalling the earlier experiments, this point is illustrated when vision is used to correct the discrepancy between proprioception in the prism experiment and between touch and proprioception in the rubber hand illusion. Most of the research in this area has become available following the KFE experiments, and therefore has not been applied to extend the findings. However, the KFE results suggest that the appropriate modality is touch which results in the recalibration of proprioceptive position sense.

Gestalt grouping principles

Although the Gestalt principles of perception have not been mentioned in specific regard to the KFE previously, it is conceivable that these rules, which have received much attention in visual and auditory perception literature, may also provide the change in perception during sensory conflict of touch and proprioception. The Gestalt

principles consist of, but are not limited to proximity, similarity, common fate and good continuation (Kelso, 1995). During the experiments by Craske (1984), these principles appear to be present to create the fusion effect. The proximity principle could describe why objects close spatially are grouped together: the button and probe. The button and probe would have also been grouped together in accordance with the law of common fate, because the button and probe moved simultaneously in the same direction.

Bayesian Inference

Bayesian Inference has been suggested to account for perceptual illusions (Goldstein, Humphreys, Shiffrar, 2005). Bayesian inference involves the idea that the world is full of noisy sensory signals that the brain must organise to perceive the environment. Because these signals are not straightforward for the brain to interpret, logical inferences must be performed to understand the current state of an individual's world. The brain uses the noisy signals to obtain the probability of the likely causes and chances of a specific situation. This information must be mapped onto prior knowledge about how the world operates. Ramachandran, Hirstein, Rogers-Ramachandran, (1998) showed that the internal model of the body is a flexible internal model, and perception is organised by making statistical correlations to generate a provisional body image. A study by Bays & Wolpert (2006) provides an example of Bayesian inference in sensorimotor behaviour.

Perceptual bias has been investigated further using the rubber hand illusion. Tsakiris, Haggard (2005) suggest that the shift in the perceived position of the arm can result from a bottom-up mechanism in which synchronous visual tactile events are

perceived as one. Bayesian principles of statistical correlation seem sufficient to extend the body representation to include even body parts as implausible as a table (Armel & Ramachandran, 2003). Only those body segments directly involved in the intersensory conflict have been found to be affected, while positional changes for the rubber hand illusion were significantly larger only for the stimulated digits because strong inference caused by the correlated sensory signals are only established for the stimulated fingers, and absent for unstimulated body parts (Tsakiris et.al, 2005).

Amodal properties

The factors that govern intermodal grouping have been linked to cognitive and sensory interaction (Bertelson, 1999). One such example comes from the spatial separation of the stimuli, where increasing the spatial separation between events in two or more modalities results in a decrease in intermodal fusion (Bertelson & Radeau, 1981). Synchrony of stimuli between the different sensory systems has also been credited with perceptual fusion, bias, and calibration of the higher order sensory signals. The “unity assumption” (Welch & Warren, 1980) refers to a process that must be undertaken by a person (and not necessarily consciously) to determine that a sensory situation indicates a single event has occurred involving discordance between two or more sensory systems. When this has taken place, the task for human perception is to restore alignment between modalities. If no discordance is detected, there is no intersensory conflict and each sensory system remains as it currently operates.

Welch (1999) presents a review of intersensory conflict and the variables that cause and resolve the disparity, for which he suggests that an intersensory bias can be

detected and resolved by the number of ‘amodal stimulus properties’ shared by the sensory systems involved. Such properties can include, but are not limited to spatial location, temporal patterning or rate, size, shape, orientation, or intensity. These variables are referred to as amodal because they are not specific to one sensory system and therefore more than one sensory system has its own perspective of the event based on an amodal property that is thought to cause the intersensory conflict and resolution. These variables may be inherent in the genetic code of humans or emerges very early in perceptual development (Kellman & Spelke, 1983; Lewkowicz, 1999). By increasing, the amodal properties between sensory systems the event is considered more likely as one, whereas decreasing the shared properties results in a reduction in the bias. By reducing the shared intermodal properties between vision and proprioception, Held & Durlach (1993) introduced a delay of visual feedback of 0.3 seconds (temporal pattern or rate) while participants watched their hand while wearing prisms which resulted in abolishing any adaptation. Therefore, while there were shared amodal proprieties, such as the size of the participant’s hand and motion, the weighting of the other variables eliminated the fusion.

Phantom sensation (The funneling illusion)

Alles (1970) describes the phenomenon of the funneling illusion,

“Two equally loud¹ stimuli presented simultaneously to adjacent locations on the skin are not felt separately but rather combine to form a sensation midway between the two stimulators”

¹ Loud in this context refers to stimulus amplitude, not sound level

Even though this paper was published before that of Craske et.al (1984), there has been no published link between these concepts and it is a distinct possibility that the KFE and the phantom sensation are similar entities of human perception. Alles describes the effect further,

“This phantom sensation is affected by the separation of the stimuli, their relative amplitudes, and their temporal order. Thus it is often described as the tactile equivalent of directional hearing”.

The effect is thought to be produced by temporal and amplitudinal inhibitions; additionally if a temporal delay is involved the successive touched position is thought to move closer to the preceding touch. If the amplitude is varied, the louder stimulus draws the other stimulus towards it (Alles, 1970). This could suggest that the KFE stimuli were considered equally loud. Hence, this information provides a theoretical framework to use for future experiments. Even without the knowledge of the funneling illusion, a fusion within the sagittal as described by Craske (1984) should not exclude any associated fusion in the medio-lateral plane. Evidence from the funneling illusion strengthens the hypothesis that a fusion may additionally occur whereby the separation of the button and probe are perceived to be significantly closer after adaptation compared to a baseline condition (no active button probe condition). These experimental ideas are elaborated within the rationale and research problems section to follow. A number of recent studies (Jongeun, Rahal, El Saddik, 2008; Mizukami, Yuchida, Sawada, 2007; Oohara, Kato, Hashimoto, Kajimoto, 2010) have replicated and applied the funneling illusion to a number of research questions.

Research problems

Can the KFE be replicated?

As of November 2010, Craske et.al, (1984) had been cited 17 times. Table 1 presents a selection of those studies that have cited Craske, Kenny, Keith (1984). To date, no study has been undertaken to investigate these findings further and to elucidate the accuracy of those findings that has been previously reported. Due to the obvious belief from the citations listed in Table 1 that this effect is both genuine and has implications for many other fields of research, it is important for an additional examination of the KFE. Those studies which cited Craske et.al (1984), and for which the interpretation of their results could change depending on results from follow-up studies of the KFE are listed in Table 1.

Table 1: Craske, Kenny, Keith, 1984

Citations

Longo, Haggard, 2010	Bianchi, Ivana; Savardi, Ugo; Bertamini, Marco, 2008
<p>“Although several researchers have identified the need for such a body model, no attempt has been made to measure this model, and its properties are unknown.”</p> <p>“Although many researchers have noted that position sense requires a stored model of the body’s metric properties”</p>	<p>“Proprioception seems to play a large role in implicit body representation in some studies”</p> <p>“The perception of our own body relies on touch, proprioception and also on visual Information”</p> <p>“The role of proprioception on healthy people’s body representations and, more precisely, on the perceived size of body parts has been demonstrated with respect to body size in general and to specific parts of the body”</p>
Ehrsson, Kito, Sadato, Passingham, Naito, 2005	Ehrsson, Holmes, Passingham, 2005
<p>“Psychophysical studies suggest that the perceived relative size of body parts depends on the integration and comparison of somatic signals from different body segments”</p> <p>“These notions are supported by the fact that people can experience illusions that the size and shape of a body part is changing when the central nervous system receives conflicting sensory signals from different body parts”</p>	<p>“synchronous tactile stimuli on two body parts can cause illusory distortions in size, shape, and location of body parts”</p>
de Vignemont, Ehrsson, Haggard, 2005	Carello, Turvey, 2000
<p>“Perceived distortions in the size and shape of body parts have been reported after various pathological conditions, during local anaesthesia of a limb or after various experimental manipulations, such as tendon vibration, in healthy subjects”</p>	<p>“Awareness of the location of the hand, for example, is thought to require stored knowledge of limb lengths together with knowledge of joint angle either itself sensed or computed from knowing where the limb started and how it was moved. Such computational accounts, however, would seem to demand that the represented body schema be impervious to the kinds of tensorial manipulations to which they are, in fact, susceptible. Once again, that susceptibility does not imply that we do not know where our limbs “really are” but, rather, is rooted in consequences of the body’s mass distribution for moving the limbs and maintaining their posture.”</p>

Graziano, Cooke, Taylor, 2000	Jones, 1988
“The body schema is made of integration of vision, proprioception, touch, and motor feedback”	“The process by which these systems undergo adaptation is not known, but Craske, Kenny, and Keith (1984) suggested that this discordance-driven adjustment and recalibration of the spatial senses are efficient means of ensuring intersensory congruence, which is necessary for accurate sensorimotor coordination”
Pagano, Turvey, 1998	
“It is commonly assumed, for example, that the coordinates of a distal extremity can only be obtained from knowledge of joint angles and limb lengths, information which must be available in the central nervous system before the initiation of movement”	
McDonnell, Scott, Dickison, Theriault, Wood, 1989	
“Craske, Kenney, and Keith have pointed out that the literature has failed to recognize that a sense of limb length is essential to achievement of motor coordination. These authors have demonstrated a significant adjustment in perceived limb length following exposure to discordant sensory information. In the case of acquired amputation, a person should experience discordance whenever the terminus of the amputated limb is used to contact the environment following recovery . The discordance probably differs for persons with congenital limb deficiency. For both types, the discordance would be altered when an artificial limb is worn, necessitating a new adaptation”.	

Perceived arm length change or perceived shift in position?

Craske & Kenny's motivation and rationale for their set of studies was that there was a lack of literature regarding how the brain processes changes in the length of limbs, such as those occurring during growth spurts, in order to attain coordinated motor behaviour. Although Craske & Kenny claim that the observed adaptation is due to perceived limb length change, here I present two alterations to the experiments to determine if this is in fact true.

1. Although joint angle was accounted for by implementing postural measurements before and after the experiment and by asking if a microlight was displaced laterally, it is insufficient to conclude that the observed adaptation was due to the *perception* that one arm was longer than the other. This is because the data that was collected was related to the *actual* movement of the arm, not the *perception* of the arm's location. As mentioned earlier, an integration of sensory systems is vital for precise perception and therefore it is likely that not only tactile but also proprioceptive sensory information would be used to estimate arm length and/or position. By touching various positions of the left and right limbs, a measurement of the participant's perceived position will be taken before and after the KFE to determine if a perceived positional change plays a role in the adaptation, rather than the previous idea of a limb length change.
2. Craske and Kenny concluded that because there was no after-effect at a point on the *right forearm*, the fusion could not result from a perceived limb position change, because theoretically a shift of the whole limb should take place. However, the data that was collected for the perceived light/touch difference at the right forearm (22.9cm closer to the body) was not compared

to a baseline before the sensory conflict was introduced. This must be seen as a flaw in their experimental design and the interpretation of results, as the participant may have actually perceived a point at the forearm to be further from the light *before* the treatment. As a result of the sensory conflict a recalibration could cause the perception that that point was actually *now* shifted forward or back (depending on where the person perceived the position during the baseline measurement). Without taking this into consideration comprehensive conclusions cannot be made from this data, and it may be possible that the perception of a kinaesthetic fusion is due to a change in limb position perception in addition to, or rather than, the previously thought length domain.

Therefore it is suggested that an enquiry into the possibility that the KFE adaptation may in fact be due to a *perceived* change in joint angle or movement of the limb forward or backward without accompanying movement in reality or perceived movement laterally. Perceived movement or proprioceptive drift of the limb when vision is not available, without actual movement has been described before in neurologically disabled patients (Wolpert, Goodbody & Husain, 1998), and healthy populations (Ehrsson et.al, 2005; Paillard & Brouchon, 1968). It is possible that *both* a perceived limb length and position change may take place, but has yet to be determined.

By touching various positions on both arms during a baseline condition (before the participant is asked to press the button), it will be possible to determine if a perceived lengthening, shortening or movement occurred. If a lengthening or shortening is the

cause, only certain aspects of the arm will be affected, which can be measured by comparing the reported distances between two touched points before and after the sensory conflict (see Figures 3a and 3b). If perceived movement of the entire limb occurs, all touched positions will have been perceived to move.

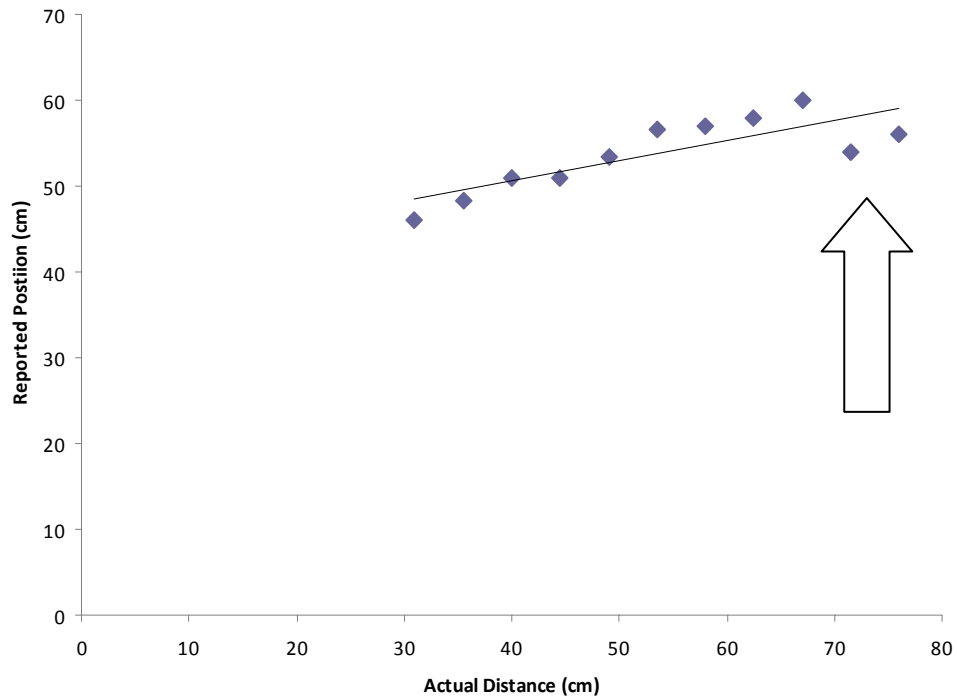


Figure 3a: Potential results: a localised length change takes place at the right finger section that is perceived to move closer to the body*

* Larger numbers correspond to positions further from the body

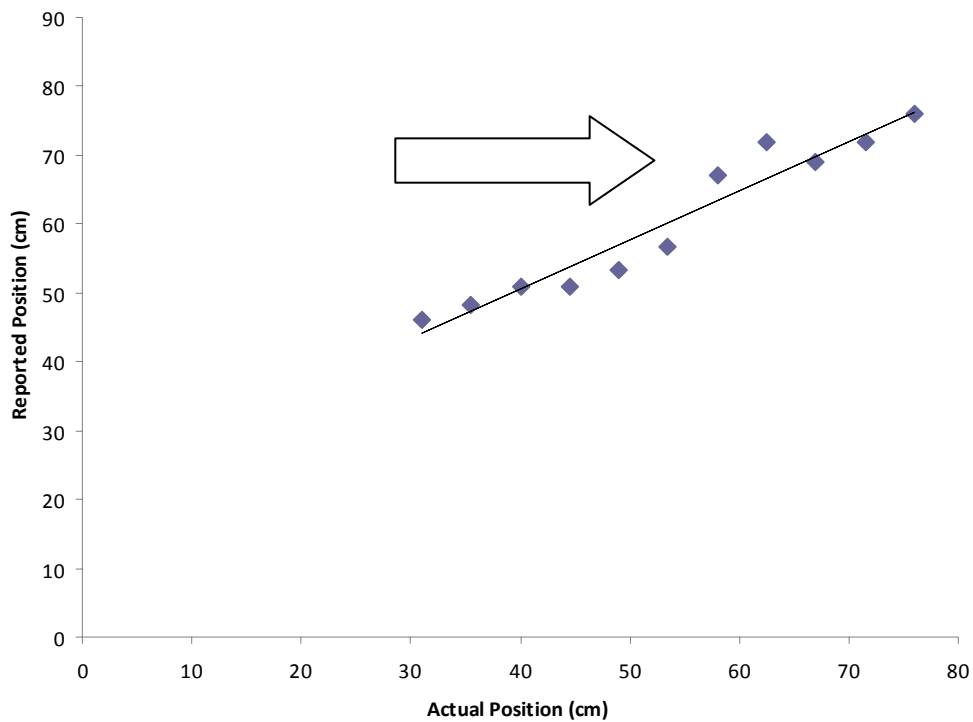


Figure 3b: Potential results: a localised length change takes place where the probe makes contact that is perceived to move closer to the body*

* Larger numbers correspond to positions further from the body

Where on the arm does length change?

If the previous authors were correct and the adaptation takes place in the length domain, what section or sections of the arm are affected? Experiment 4 of Craske (1984) may provide a potential avenue for this question to be answered. After fusion to the 12.7cm probe discrepancy, the participants were touched at a point on the right forearm 22.9cm closer to the body than the fingertip. The participants were asked to estimate where they felt the touch in relation to a light directly above. The authors found that the adaptation had vanished where they perceived the touch to be within 0.18cm of the light. This was significantly different to that found at the wrist, where

the perception was a difference of 1.69cm, whereas the difference between the right thumb and the light was even larger at 3.4cm. These results suggest that some aspects of the arm are affected by the adaptation more or less than others. This may be similar to that of reports of a 'telescope limb', from phantom limb sufferers (Ramachandran et.al, 1998). 'Telescoping' affects some aspects of the arm more than others. This is when the arm is perceived to vanish, leaving just the perception of a hand connected to the shoulder or, alternatively, floating by itself in space. From preliminary results, of Craske (1984), it seems evident that the areas close to the button and probe during the adaptation to sensory conflict are those where the perception of a limb length change occurs (a localised effect). This statement is made so readily because regions of both arms from the wrist to the fingertip are perceived to change position, whereas regions further back towards the body (22.9cm) that were not stimulated by the probe remain unaffected. To answer these questions, a range of regions on the medial aspect of both arms can be probed before and after adaptation. The participant will be asked where they feel the touch in relation to a grid above the arms; there may be an effect where large discrepancies for values near the site of probing and pressing before and after the treatment, whereas areas that were not touched during the sensory conflict receive the same reports as baseline measurements (Figures 3a and 3b). The right arm (index finger touched by button) may change primarily distally, whereas the left arm (probe touches wrist) may have changes closer to the elbow. Although the data collated by Craske (1984) is helpful to understand the KFE, another two flaws in the methodology and interpretation were identified, and will be addressed. After-effect judgements were only measured closer to the body compared to the testing site on the *right arm*. No rationale was provided for this, and it is again possible that an effect

could have been missed, in this instance on the left arm, especially because this is the arm that was being probed.

The authors made conclusions at the end of their paper that the fusion after-effect is only sensitive on the patch of skin that was stimulated by either the button or probe. The results they present actually counter this because when the left wrist and right fingertip participated in the fusion, the participants still perceived shifted difference between a light vertically above a tactile point on the right wrist (1.68cm), which did not receive any treatment. Therefore, it is possible that regions of the arm not involved in the treatment can undergo perceptual changes. With these thoughts in mind, an investigation to detail where the apparent arm lengthening and shortening changes take place, after taking baseline measurements for both arms, should allow a clearer picture of the KFE. After the person has been exposed to the kinaesthetic fusion device, if the distance between two touched points has increased or decreased, it can be determined which segment of the arm has been affected.

Tactile/proprioceptive bias and acuity of the arm, hand or finger during visual occlusion

A number of recent studies have investigated the acuity and bias of proprioception information of the hand during visual occlusion. The design of this experiment will allow comparisons and extensions to the existing knowledge in this area. At present, there has not been a study that has investigated tactile acuity for positions on the forearm, hand or finger. What has been shown by Van beers, Sittig, van der Gon (1998) and Wilson et.al (2010) is that proprioceptive acuity of the hand decreases for positions further from the body. The current hypothesis is that when a position is

touched closer to the body, for example, a position near the elbow will have less intra-subject variability than a position on the fingertip when the elbow is at 90 degrees and the forearm is positioned straight ahead.

Does the fusion occur in the medio-lateral plane?

As Craske et al (1984) described the KFE, the reader forms a picture in their mind where two points that are separated in the sagittal direction by 12.7cm, are perceived to move towards each other during repeated tactile exposure. Because these two points are located on the left and right hands/arms they are not only separated in the sagittal direction but also in the medio-lateral direction; hence a fusion in this direction may have, and it is logical to propose has, taken place. The method of measurement of the perceived touched positions presented here will allow the answer to this question to be formulated. Not only can measurements be taken in one dimension but also a second dimension can be added. A history of investigating the perception of two simultaneous touches to the skin has been addressed. Von Besksey's (1967) discovery of the "funneling illusion" which was described in earlier sections has provided a theoretical basis for this enquiry. There is no reason why a fusion should not occur to the same extent as the anterior posterior direction (because the distances are essentially separated by the same distance, in different directions).

Are there order effects for judgments when one condition is preceded by another?

Experiments can be counterbalanced to control for time-related threats to internal validity. Craske et al (1984) did not counterbalance their experiments, and this can be seen as another flaw in their methodology and design. How can the reader be sure the effects reported are not due to time related events such as proprioceptive drift (Wann, 1992), or the perceived shortening of the limb during visual occlusion mentioned by Gross et al (1974)? Until the experiments are counterbalanced, the argument that two separated tactile points cause the KFE cannot be validated. Therefore in the experiments to be presented, half the participants received the control condition (0cm displacement) first and the other half received the experimental condition first (12.7cm displacement). Any such changes after testing will clarify interpretation.

A new methodology

Proprioceptive acuity research has faced a challenge in the past, whereby difficulties in interpretation of results have arisen due to the knowledge that proprioception, like vision, is processed differently for perception and action. This was recently highlighted in a paper by Wilson, Wong & Gribble (2010), who aimed to introduce a new method that avoided active movement and interactions with other sensory systems. The participant's made decisions concerning the location of their hand in relation to a remembered proprioceptive reference point. A second experiment used a visual point to evaluate and control for memory influencing the data during the proprioceptive reference point judgment. Measures of proprioception will continue to be used and therefore issues of validity and reliability for the methods used are important. The present study requires the participant to have both limbs concealed from vision and therefore a method not previously utilised will be introduced.

To eliminate any threat to internal validity in this study, a reference grid will be provided above the limbs for the individual to select a position they perceive to be directly above a touched position on their arm, hand or finger. This will allow accurate measurement of the magnitude of the KFE and minimise inter-subject variability. Instead of using a staircase method to gain an understanding for where the participant perceives certain positions on the limb, here the participant is asked to select a 0.95cm x 0.95cm square they perceive to be directly above a touched position. To do this the participant will report a letter followed by two numbers within a square; for example, K78. Once data is collected, a scatterplot representing the perceived position of both limbs can then be displayed to enable an insight into participants' positional awareness of their limbs without visual feedback, during not only the experimental manipulation but the control condition and baseline conditions.

Another reason for the design and method choice of measuring perceived touched position was to advance the technique that was used in the experiments directly related to this project (Craske et al, 1984). The analysis that was used to measure the participant's perception of their arms could be enhanced by reliable methods for the estimation made, and this may result in alternative interpretations of the results. The method of measurement did not appear to be reliable, due to the participant's subjective estimate for the distance of the probe to the opposite fingertip in inches. Both papers in 1981 and 1984 did not mention the collection of any data that recognised if there was consistency within or between participants. It remains unclear if the participants could consistently report the same distance for a single location and therefore the spatial accuracy of the estimates is ambiguous.

Research Aims and Objectives

This project aimed to:

- Replicate the kinaesthetic fusion effect (KFE) reported by Craske et.al, 1984 and;
- If replicated, to determine if the KFE is also associated with a perceived change in length and/or position of the limbs
- Investigate whether or not a similar illusion fusion occurs whereby the limb separation (medio-lateral plane) is perceived to be reduced
- Provide a robust methodology to measure the effect in the sagittal and medio-lateral planes
- Determine / measure / investigate the degree of tactile/proprioceptive acuity and bias for various positions on the arm, hand and finger during visual occlusion, which may be applicable to future research

Method

Participants

Participants for this experiment were recruited from Queensland University of Technology. In total 16 individuals participated (9 male and 7 female participants). The number of participants selected was based on similar research projects (Craske et.al, 1984), and power calculations. Power is the probability of rejecting the null hypothesis when the null hypothesis is false (type II error) (Thomas, Nelson, 2005). Statistical power calculations (alpha 0.05) indicated that with an effect size (Cohen's D) of 0.7 which was obtained by Craske (1984), meant approximately a sample size of twelve participants would be required to obtain an 80% probability of not making a type II error (Cohen, 1988). All subjects participated voluntarily and were not reimbursed. Subject ages ranged from 19 to 32, mean 24.2 years. Participants over the age of 40 were excluded, as there is evidence that proprioception acuity decreases after this age (Connelly, Montgomery, 2001). Subjects had no prior experience with tactile or proprioceptive experiments. Subjects who did not state any relevant, sensory, motor or cognitive medical conditions that might affect their ability to participate in the experiment were included. In the recruitment flyer (appendix), potential participants were advised that they would only be able to participate if they had no prior injuries to the arms or nervous system. Handedness was not considered as a criterion for inclusion or exclusion. Participants were not informed of the expected results or hypotheses. Participants were debriefed at the conclusion of testing regarding the true purpose of the study. The Queensland University of Technology Human Research Ethics Committee approved the study and written informed consent was obtained from all participants prior to data collection.

Apparatus

Participants sat in a chair with a seat height of 40cm, at a desk with surface dimensions of 54cm x 65cm and a height of 71cm. A 39cm x 65cm wooden surface was secured in place at a height of 15cm above the desk surface, which allowed the participants to have their arms placed underneath to occlude visual information about limb positions throughout the experiment. This height separation of 15 cm has been used for other proprioceptive acuity experiments (Gross, Ross, Melzack, 1974). Pilot studies were undertaken to ensure that the physical layout of the apparatus would allow each of the tasks required for the conduct of the study, such as providing the experimenter enough room to be able to reach and touch the participant's arms and hands. It was also important for the experimenter to have a clear view of the arms so if any movement occurred it could be repositioned, by aligning pen markings on the arm and hands to reference marks that were laid down at the start of testing. The experimenter would also need to see the arms to note if the probe was contacting the arm when the button was pressed. A 65cm x 41cm box was built around the surface (Figure 4).



Figure 4: A participant sitting in the apparatus, with a cloth draped around the neck to prevent vision of the arms

The box was open at the end where the participant sat, to allow viewing of a grid above the arms. The purpose of the box was to prevent the participant from gaining location cues when the examiner touched the limbs in later parts of the experiment. A grid was glued flat to the surface covering the subject's arms. The grid which covered the entire surface contained approximately 2200 squares ($0.96\text{cm} \times 0.98\text{cm}$). In each square, a code consisting of a letter followed by two numbers allowed participants to select a square they perceived to be directly above the touched position on their arm. The grid codes were randomised to decrease the likelihood of participants using memory strategies when making location judgments and to prevent inferring a

position by extrapolation from neighbouring positions (Figure 4). The room was well lit which allowed the squares to be seen easily.

R60	O8	F37	E40	K84	I99	J95	B55	W88	T57	H23	H50	Q97	U91
J73	E97	S83	X65	R63	U61	Q2	L78	O60	L61	U54	L58	P31	J7
A22	R36	C22	I32	W87	B97	Y32	R16	W11	K85	O36	B4	E94	Y24
K9	X87	R99	D99	T39	K77	C93	X5	F9	T23	G22	M34	Q9	G40
H29	T50	N56	R34	X58	F46	R74	W59	Z32	J63	Y2	C19	A41	G83
Y93	R66	A79	V75	L41	X14	M2	A12	D19	Q30	L31	E16	H95	O9
R73	C3	S99	W61	Y23	J71	O50	X50	M54	R15	S9	Z2	U88	F7
H93	X18	G4	T20	X98	H6	U55	X26	Z18	P75	O73	K18	F65	F89
U84	C49	U74	E81	S64	O30	U18	S57	S62	Y95	F81	T16	F31	V1
X67	B82	B62	J85	I40	G52	H65	U32	I83	K12	Q90	L10	S67	Z1
M1	V63	V44	U95	B67	A78	N36	I35	Q93	Q48	A65	O72	L16	B4
U10	Y51	L73	K23	T54	E1	J41	Z34	G36	I76	F96	O28	F26	F7
P84	W7	N44	H88	J6	X81	T30	H18	E56	Y12	D16	D72	T88	J1
E52	E42	S46	U57	W56	U79	C79	N86	L77	S54	L15	L63	N52	T6
Z22	U59	Q96	C60	A45	P87	A71	B94	U94	U82	I24	M32	X44	T4
P1	J12	I89	G16	Y6	P2	G86	W79	Q60	W16	E32	J28	B72	M
X82	O95	Q42	S16	R58	K73	I65	R1	S63	D34	J98	P12	L92	X3
I18	C80	E77	B47	R54	Q71	Z60	H89	K22	O49	Q98	Q16	A87	T2
V6	B1	E35	Y82	J39	M52	Z10	T46	R23	K91	H68	D89	P70	F9
6	G65	R44	U31	P46	M3	C4	F32	U23	S15	W60	W86	S47	Q

Figure 5: A section of the Grid above the arms used by participants to estimate the perceived touched position

Coordinate system

The grid used a Cartesian coordinate system with the medio-lateral and sagittal axes as the two dimensions. The origin of the coordinate system was the top left hand corner of the surface (0, 0). Therefore, medio-lateral values increased to the right of the origin from the participant's perspective and sagittal values increased towards the participant. Each square was represented in a spreadsheet in the same layout as the scale that the participants saw above their arms. To convert participant reports into actual coordinates in centimetres an Excel Lookup function was developed which returned a value from a range (one row (sagittal) or one column (medio-lateral)) for each box. This value was then converted into actual coordinates, in centimetres, from the origin. Each axis of the coordinate system was analysed separately.

Arm support

The arms rested in wedge-shaped foam support that allowed the arms to remain in the same position throughout the experiment (Figure 6). The foam also permitted the index finger to rest horizontally next to a button that was located medial to the right arm. The left index finger rested in a mirror image position on the opposite side of the apparatus; however, a probe was directly adjacent to the limb. A circular sticker was positioned on the foam that indicated where the participant needed to keep their finger positioned throughout the experiment and to prevent any slight movements. The foam was raised by approximately three cm from the table surface which caused the arm to move three cm closer to the surface above their arms. The arms were in a position half way between supine and prone and the elbow was flexed to 90 degrees (figure 4).



Figure 6: Hands positioned into wedge shaped foam support

Solenoid probe device

The ‘solenoid probe device’ sat directly in between the left and right arms (Figure 7).

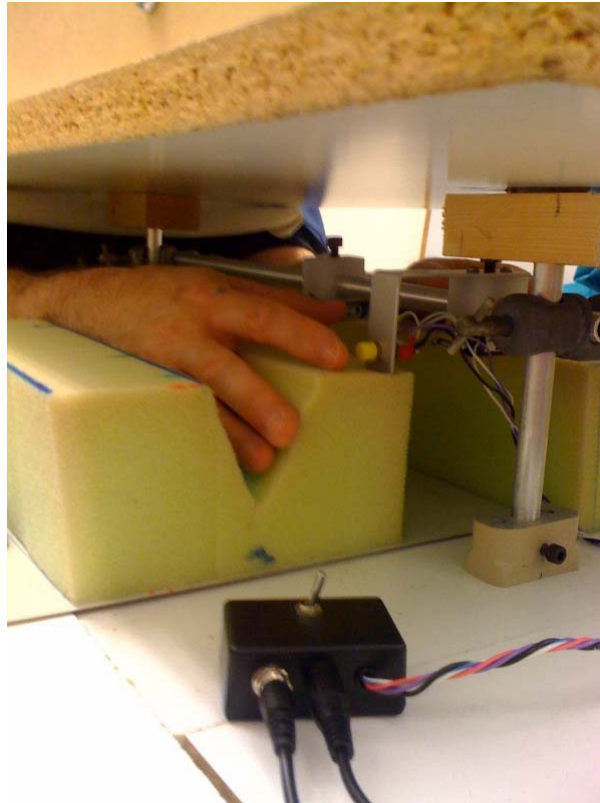


Figure 7: The solenoid probe device sat between the arms

The device was modeled on the work of Craske et.al (1984). The button and probe were connected to a thin metal tube that sat between the arms of the participant. The tube sat approximately 10cm above the table surface so contact with the hand was possible. The button probe distance in the horizontal dimension stayed constant at 12.7cm. However another probe was located 12.7cm closer to the body, which when activated by the button adjacent to the right index finger, could independently make contact with the participant's left arm, without activating the probe directly across from the button. The button was circular, had a diameter of 0.5cm whereas the rubber

solenoid probes were 2.5cm long, and had a diameter of 0.3cm. The device could be moved up or down depending on the participant's anthropometrics, however the button and probe always remained in the same position for all participants. Participants wore headphones (Figure 8) which were connected by a two-metre wire to a small electronic circuit box. As the button on the solenoid probe device was pressed, a high pitched buzz was heard by the participant through the headphones and therefore occluded any sound caused by the probe movement as this could provide the participant with auditory location cues



Figure 8: An example of the participant in position wearing headphones

Procedure

Data collection was undertaken in a single one and a half hour session. Testing took place in a laboratory at the Institute of Health and Biomedical Innovation, QUT. After subjects were informed of the instructions of the study, and had any questions answered, they filled out a “Voluntary Consent Form” (appendix).

Participant Setup

Subjects were asked to remove all jewellery and/or watches. If the participant was wearing a coat, they were asked to either roll the sleeves up or take the coat off. The participant was then seated in front of a desk so their arms could rest in front of them and length measurements could be taken. The participant wore a blindfold as the examiner measured the arm length from the index finger tip to the elbow crease with a standard tape measure. The length of each individual’s left and right hand and arm (index finger to elbow crease), was then entered into a Microsoft Excel spreadsheet on a computer to inform the experimenter where 20%, 40%, 60% and 80% of the arm length was located. 0% was treated as the most distal aspect of the index finger. The formula that was used in excel was:

= percentage location*arm length

For example for an arm length of 42cm, 40% would equal (= 0.40*42)

Each point was then marked out with a blue highlighter, so touches to that location would be consistent. The blindfold was worn to ensure no individual was aware of the location of any pen markings on their arms. Once 10 markings (5 on each arm) were completed, the participant was directed to the testing apparatus, while wearing the blindfold. Subjects were seated in a non-swivel, non-height adjustable, comfortable

chair, which had a backrest. However, participants were told to sit leaning slightly forwards so they could have a better view of the grid. A top down view of the apparatus is shown in Figure 8. The participants were then instructed to completely relax both arms by their sides while the experimenter passively moved each limb on top of the table (below the surface that contained the grid).

Once the arms were in position, standardised instructions were read to the subjects by the experimenter. A green sticker was placed at the end of the box on the midline. This sticker was used to remind participants to remain aligned with the sticker, as significant head movement could influence judgments of arm position (Hodges, Knox, 2005). This would also control for any head movement variation where post analysis gaze angles could be calculated. If the participant wore glasses, they were permitted to be worn. Subjects were encouraged to forget past estimates of position and to treat each judgment as independent of those that had occurred previously. The experimental design was setup in this way to prevent any participant bias.

Additionally participants were reminded that they were allowed a break at any stage during the experiment, and they could easily be positioned back if need be.

Nevertheless, each participant completed the experiment without interruption. The instructions also included a reminder that the experiment required attention and concentration at all times. If the participant was having trouble making an estimate, they were informed that looking in the direction of the probed position can improve acuity (Kennett, Taylor-Clarke, Haggard, 2001), but they should still report the position they believed to be directly above the touched position. Once instructions were delivered, the experiment began. Testing procedures are described below. As the first condition (baseline) ended, the participants were instructed on the next aspect of the experiment. Before the conditions involving the button, pressing the examiner

mimed the flexion movement of the right index finger that would allow the participant to depress the button and activate the solenoid probe. Participants were then allowed to practice pressing the button without the probe circuit activated before data collection began.

Testing procedure

Participants were tested under three conditions. 1) Baseline, 2) Button and Probe directly opposite (0cm displacement condition), and 3) Button and Probe separated in the sagittal plane, where the probe (left arm) was 12.7cm closer to the body (12.7 cm displacement condition) (Craske et.al, 1984). To eliminate any order effects eight participants were randomly allocated to the following order:

Baseline ----- 0cm condition ----- 12.7 cm condition

And the remaining eight were randomly allocated and tested under the following order:

Baseline ----- 12.7 cm condition ----- 0 cm condition

Baseline condition

During the baseline measurements, the examiner with a wooden dowel, diameter approximately 0.5cm, lightly touched the participant. The participant's task was then to report where they felt the touch in relation to the grid. Participants had to select one square by reporting the code in the box (eg. K78) they perceived was directly the touched location. The order in which the five positions on both arms were touched

had been randomised prior to the experiment for each participant, to minimise any memory-based judgments. In addition, during the instructions the participants were asked to make judgments independent of preceding estimates. Each position was touched three times interspersed with the other positions prior to commencing the next condition. The examiner kept the dowel on the touched position until the participant provided a response. This was intended to reduce any individual differences in responses associated with inter-subject variations in short-term memory for presentation of the stimulus.

0 cm probe displacement condition & 12.7 cm probe displacement condition (active button probe condition)

Following the baseline condition, the participant was either assigned to the group that undertook the 0 cm probe displacement condition or 12.7 cm probe displacement condition. In each condition, the participant was instructed to press the button by slightly flexing the right index finger. After pressing the button 10 times sequentially with a gap of one to two seconds between presses, the participant was instructed to report where they felt they were pressing the button and where they felt the probe touch them in relation to the grid. This process continued for another five trials and the button was pressed a total of 60 times. This constituted one block. Having completed one block, the examiner asked the participant to cease pressing the button while the 10 locations on both arms were passively touched (this process will be known as the ‘passive touch process’). Again, the participant’s task was to report where they now felt the touch. Once each position was touched and an estimate recorded, the participant was instructed to press the button another 10 times, until another block was complete. The same procedure as outlined for the active button

probe condition was followed for another two blocks for a total of three blocks for both 0cm and 12.7cm conditions. A flow chart of this process is outlined on the next page (Figure 9).

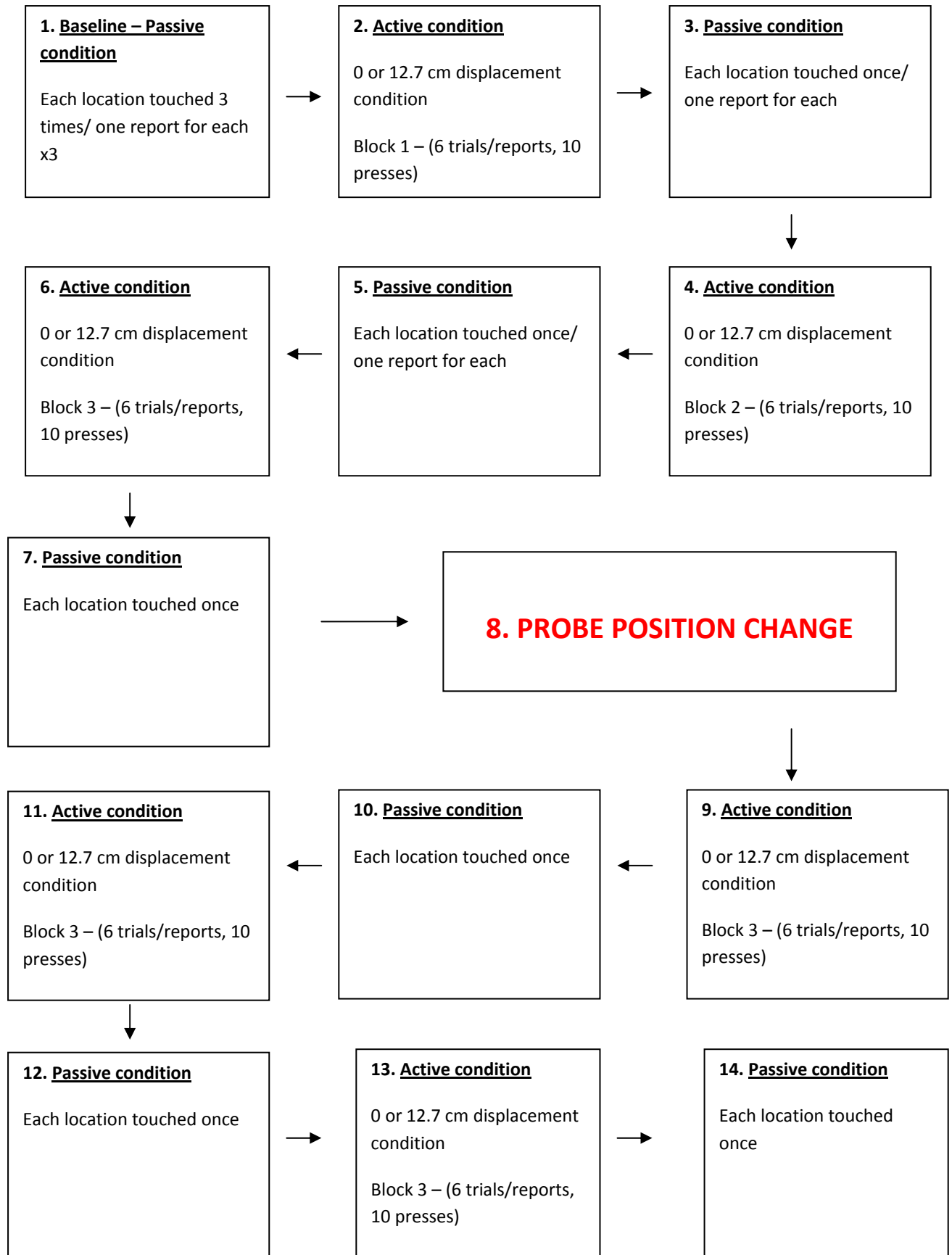


Figure 9: Experimental Design

Internal validity

Internal validity was preserved by ensuring consistent testing during the three conditions and between individuals. Proprioceptive accuracy has been shown to be influenced by joint position (Rosetti, Meckler, Prablanc, 1994); whether an individual is exerting an isometric contraction during testing (Rymer and D’Almeida, 1980); if the limb was actively or passively placed into position (Paillard and Brouchon, 1968); whether tactile information is available during localisation (Paillard and Stelmach, 1999); and temporal presentation of the stimuli. These factors were taken into consideration when planning and testing each participant and kept as consistent as possible. Additionally, visual and auditory cues needed to be controlled. Participants sat in a quiet room to prevent distraction from the task and wore headphones that were connected by a 2m cable to an electronic circuit. The circuit processed the voltage change when the button was depressed on the kinaesthetic fusion device to produce movement of the solenoid. A sound generated over the headphones masked those from the solenoid on each occasion the button was pressed. The solenoid probe device was covered with a sheet before the participant sat in place to prevent the participant seeing the displaced probe. Once the arms were in position a sheet that was connected to the surface of the table was wrapped around the participant’s neck to prevent arm position cues. The box which surrounded the surface ensured the prevention of additional cues that may be provided if the participant could see the position in which the examiner assumed to touch the limbs with the wooden dowel.

Limitations

There may be slight measurement error within the data collected for the actual position of the limbs. The values for each of the five positions on the arms were collected by the examiner using a setsquare by aligning the marked position with the surface above the arms for both the sagittal (the long side of the surface) and medio-lateral (short side of the surface) axes. A mark was made on the surface that corresponded to that position and was later measured after the participant had left. All measurements were taken from the origin of the surface in the top left hand corner. The use of a high-resolution three-dimensional tracking system in the future would prevent any uncertainty in data collection.

To generate unambiguous evidence of a causal effect of a condition, a third phase of testing is usually added to an experimental design. The ABA design provides evidence that an experimental treatment condition and not some other extraneous variable caused a given behaviour. The design involves measuring a dependent variable during a baseline condition to compare against the experimental condition, which follows. Once the experimental condition has concluded, the baseline condition is then reinstituted. The experiments presented here could not employ this type of design, due to the associated time cost of adding an extra condition.

Research design, data reduction and analysis

The research design was set up as within-subject design, to minimise the overall duration of testing. All participants were randomly sampled and randomly assigned to one of the two groups (0 cm displacement condition first or 12.7 cm displacement condition first). An example data entry sheet that was used by the examiner can be found in the Appendix.

Data was collected using pen and paper so the examiner could touch the arms at the desired positions in between recording. A copy of the data collection sheet can be found in the appendix. As the participant reported a square by its code, this was written into the sheet by hand. Once the experiment had finished and the participant had left, the data was entered into an identical spreadsheet in Excel which contained equations to convert the codes, first into an Excel-based coordinate system in the medio-lateral and sagittal planes and then into actual positions in centimetres. Means were then obtained from the three baseline passive touches for each of the 10 locations and for the other two conditions. Means were also collected for each block during the active button and probe condition. Each participant means were then entered into a separate Excel data file and separated into condition and position. The data from this file was entered into SPSS to test for differences. Individual trials for which the perceived position was greater than two times the standard deviation from the mean were considered outliers and removed from further analysis. All data was inspected to meet the parametric data assumptions of homogeneity of variance, normal distribution, interval data and independence. Friedman's test or the Wilcoxon signed-rank test was used if assumptions were not met. If sphericity was not met, a Greenhouse-Geisser adjustment was used. Cohen's D effect size was calculated for

any significant differences. All alpha levels were set at <0.05 . A summary of the statistics can be found in the next section.

Independent variables

There were four independent variables, Condition (3), Order (2), Arm (2), and Location (6).

Dependent variables

The primary dependent variables that were used were obtained by recording each participant's perception of five positions on the left and right arm. These positions were marked after measuring from the elbow crease to the index finger of each participant. Five positions were then marked out on each arm as 0%, 20%, 40%, 60% & 80% of arm length (Figure 10). 0% was the most distal part of the arm (index fingertip).

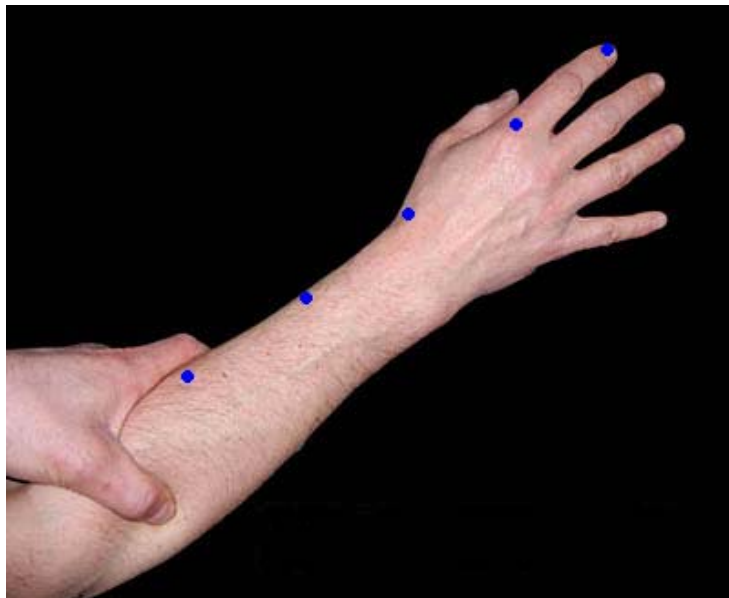


Figure 10: Approximate five markings for the right arm

The position for where the individual perceived they were pressing the button was also included as was where they felt the probe at a 0cm displacement and 12.7cm displacement. Data was collected throughout the experiment for the participants as many times as possible in a reasonable timeframe, because it has been established that increasing the number of trials increases the statistical power and stability of the derived variables (Allison and Fukushima 2003). This experiment assessed errors and acuity separately. Errors provide information related to the currently perceived position of a touched skin location, however this measurement does not reveal the noise within processing of the tactile/proprioceptive signals. Larger variability reflects the noise in the system. Variable Error embodies the variability of errors in several trials and according to the general psychophysical definition of the sensory discrimination threshold (Gescheider, 1997) it is considered to reflect the acuity of sensorimotor processes (Clark, Larwood, Davis, Deffenbacher, 1995). Variable Error is calculated as the standard deviation of the differences between the perceived position and the actual position for a number of trials. Therefore, the standard deviation of the participant's reports or Variable Error was used as a measure of acuity. Constant error took the sign (direction of error) into account that represented the response bias or the systematic tendency to over or underestimate the stimuli. The medio-lateral and sagittal planes were calculated separately. Reported limb separation was also derived from the data for analysis.

Statistics

Analysis one – A Comparison of perceived locations of button and probe during active condition

Right index finger (Button)

Independent variable:

1. Condition (3) – Baseline, 0cm probe displacement, 12.7cm cm probe displacement

Dependent variables:

2. Sagittal coordinates
3. Medio-lateral coordinates

One way repeated measures ANOVA, LSD post hoc test

Left index finger (Probe)

Independent Variable:

1. Condition (2) – Baseline, 0cm probe displacement

Dependant variables

2. Sagittal coordinates
3. Medio-lateral coordinates

Paired T-test

Left 12.7 cm probe position

Independent Variable:

1. Condition (3) – Baseline, 0cm displacement, 12.7 cm displacement

Dependant variables

2. Sagittal coordinate
3. Medio-lateral coordinate

One way repeated measures ANOVA, LSD post hoc test

Analysis two

Comparison of perceived passively probed locations

Independent Variables

1. Condition (3) – Baseline, 0cm displacement, 12.7cm displacement
2. Location (5) – Fingertip (0%), 20%, 40%, 60%, 80% of arm length
3. Arm (2) – Left and right

Dependant variables

1. Sagittal coordinate
2. Medio-lateral coordinate
3. Left and right fingertip separation (medio-lateral plane), 12.7cm probe area
and right index fingertip separation (medio-lateral plane)

4. Absolute, constant and variable Error from actual position – (sagittal and medio-lateral coordinates)

Three way repeated measure ANOVA, Bonferroni post hoc test

Results

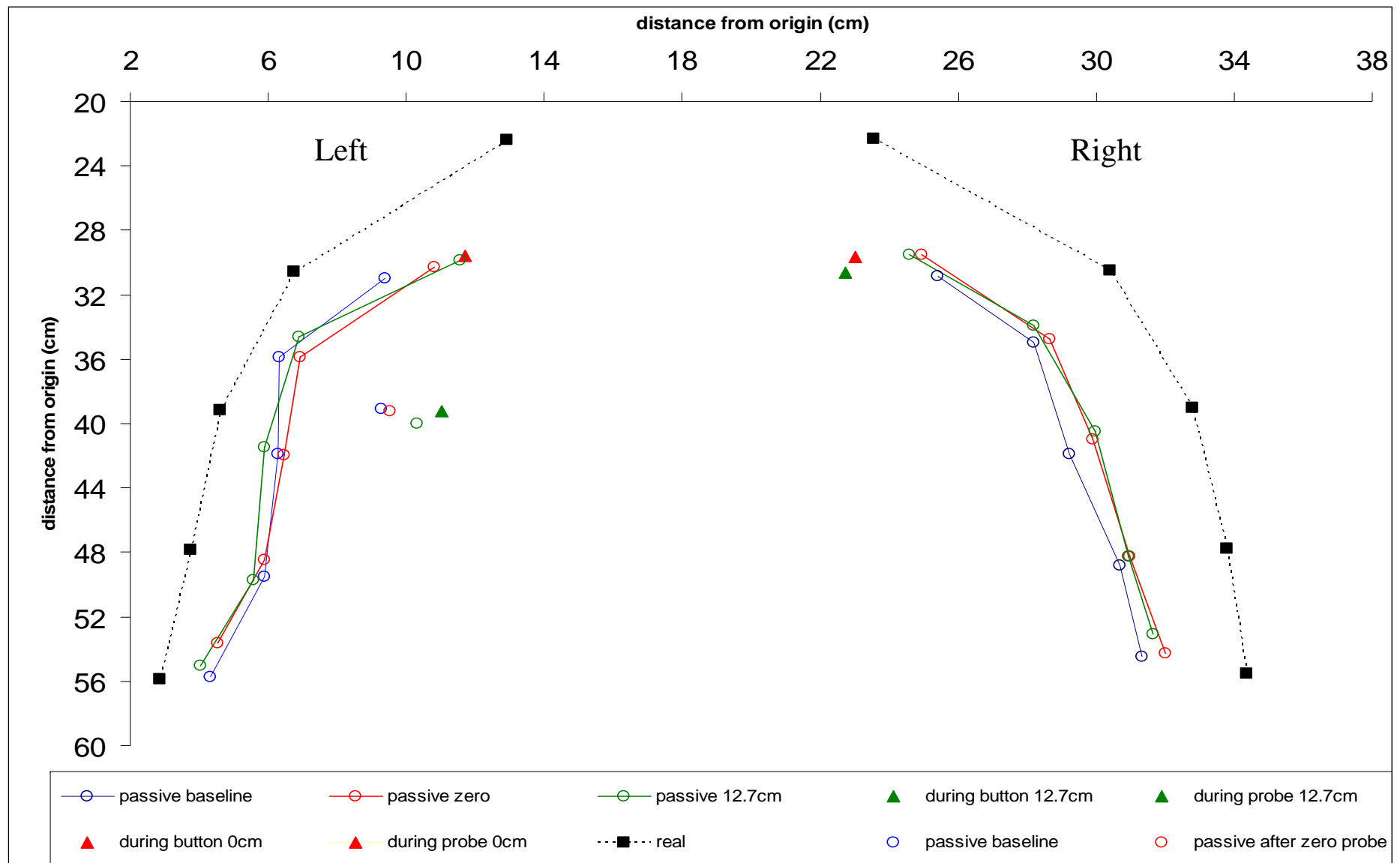


Figure 11: A two dimensional representation of the five actual and reported touched positions for the left and right limbs.

“Foreshortening” effect

Before presenting the main results that bear on the question of the KFE, an important aspect of the reporting method will be outlined. Figure 11 shows a large and systematic shift – medially and towards (Figure 12) the body – of all reported positions relative to their actual locations.

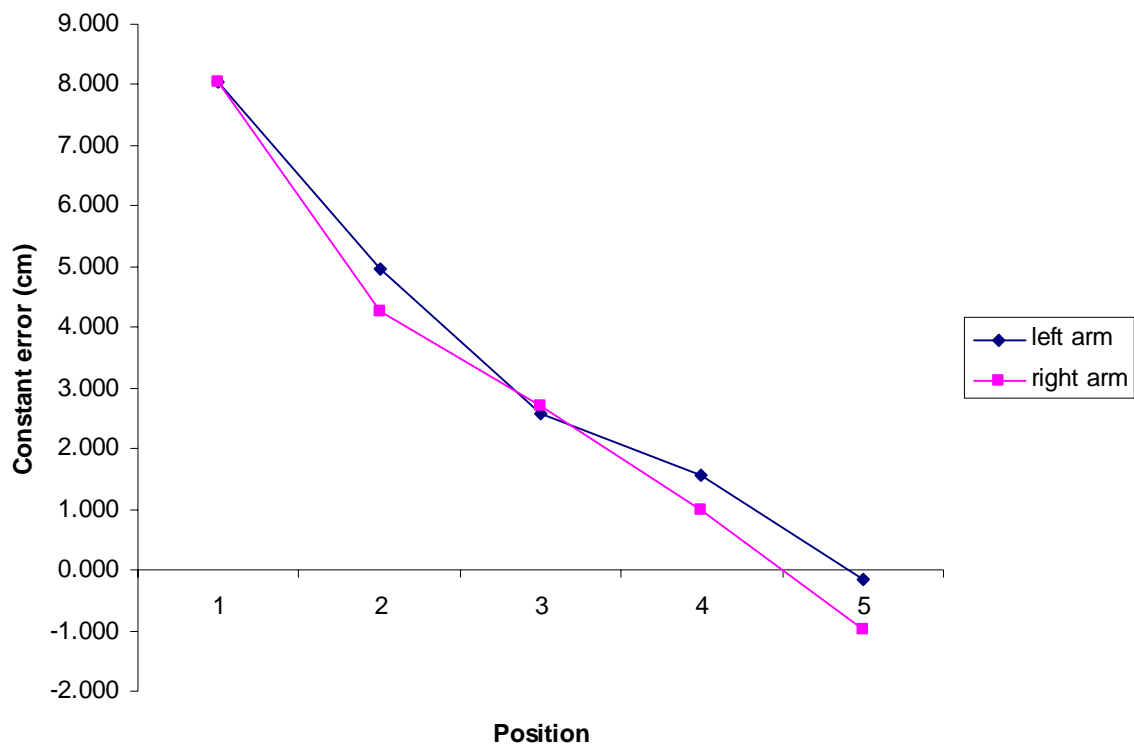


Figure 12: Constant error during the baseline condition for reported position (sagittal plane)*, **

*position 1 corresponds to 0% of arm length, 2 as 20% etc.

** Positive numbers correspond to positions closer to the body, negative numbers correspond to positions further from the body

If taken at face value, this would indicate that there were significant shifts in the perceived locations of various parts of the two limbs throughout the experiment. However, an aspect of the reporting method may account for these differences.

Figure 13 shows in diagram form the relationship between the sagittal location of the index finger-tip resting on the surface (Y1 in Figure 13), and its projection along the line of sight to the surface, 15 cm higher, of the reporting grid. If participants made their judgments about any limb location by a “visual” judgment (i.e. imagining where, in visual space, the limb would be if it were not occluded), then the reported position on the grid would correspond to a “foreshortened” position (shown by Y2 in Figure 13).

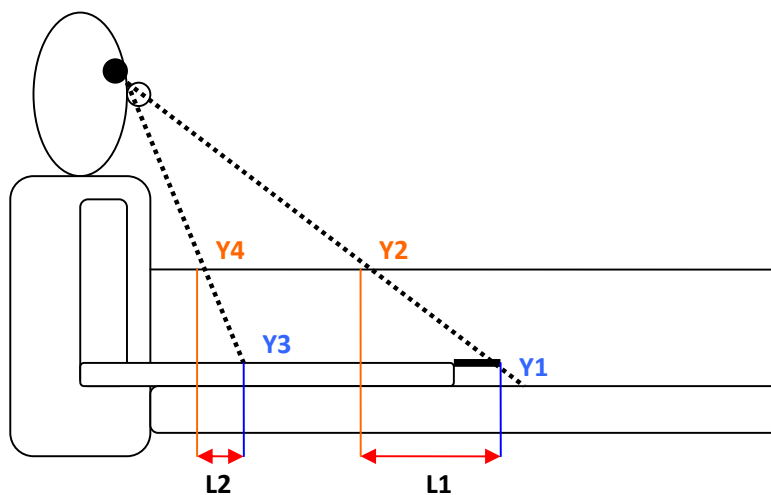


Figure 13: The “foreshortening” effect (sagittal plane)

To test this possibility, the typical three-dimensional position of the participant’s head (midway between each eye) was estimated. The known average actual positions touched during the experiment (0, 20...80% positions) were then expressed in adjusted sagittal and medio-lateral coordinates (i.e., by their projection along this notional line of sight). Also taken into account

was the height of these positions relative to each surface, due to the nonsymmetrical nature of the limb, which resulted in the height of the touched positions, varying. The results of the analyses for the sagittal and medio-lateral planes are shown in Figure 14 and 16, in which the reported and transformed line of sight data are shown in a scatter-plot and the linear regression was calculated. In Figure 14, position 0% of arm length starts at approximately 31cm and subsequent positions follow in order, as the distance from the origin increases. In Figure 16, the data points for the left and right arms are found at either end of the graph. For each arm, as the gradient increases the corresponding position of arm length increases

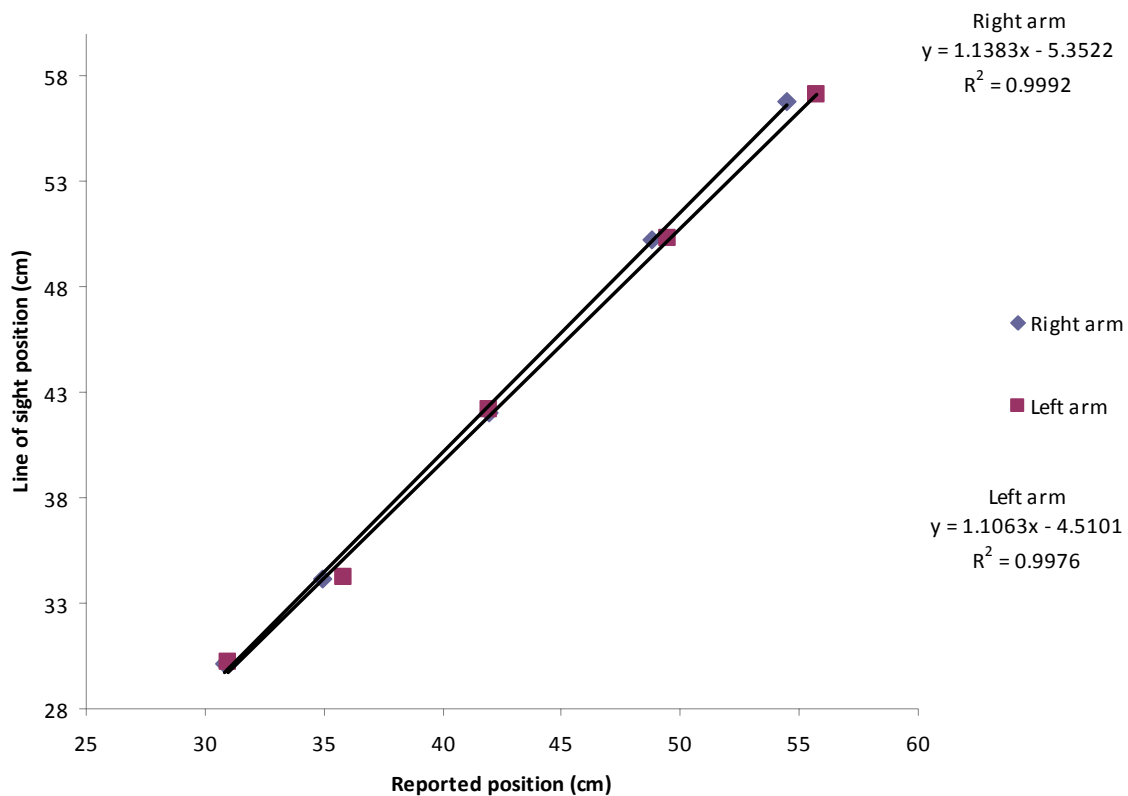


Figure 14: Transformed line of sight and reported positions for the left and right arms (sagittal plane)

Figure 15 shows in diagram form the relationship between the medio-lateral location of the position 20% of arm length resting on the surface (X1 in Figure 15), and its projection along the line of sight to the surface, 15 cm higher, of the reporting grid. If participants made their judgments about any limb location by a “visual” judgment (i.e. imagining where, in visual space, the limb would be if it were not occluded), then the reported position on the grid would correspond to a medially “foreshortened” position (shown by X2 in Figure 15).

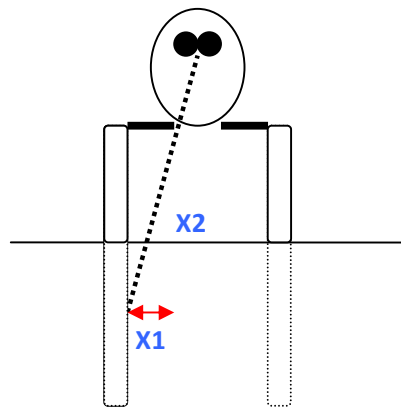


Figure 15: A frontal view of the foreshortening effect (medio-lateral plane)

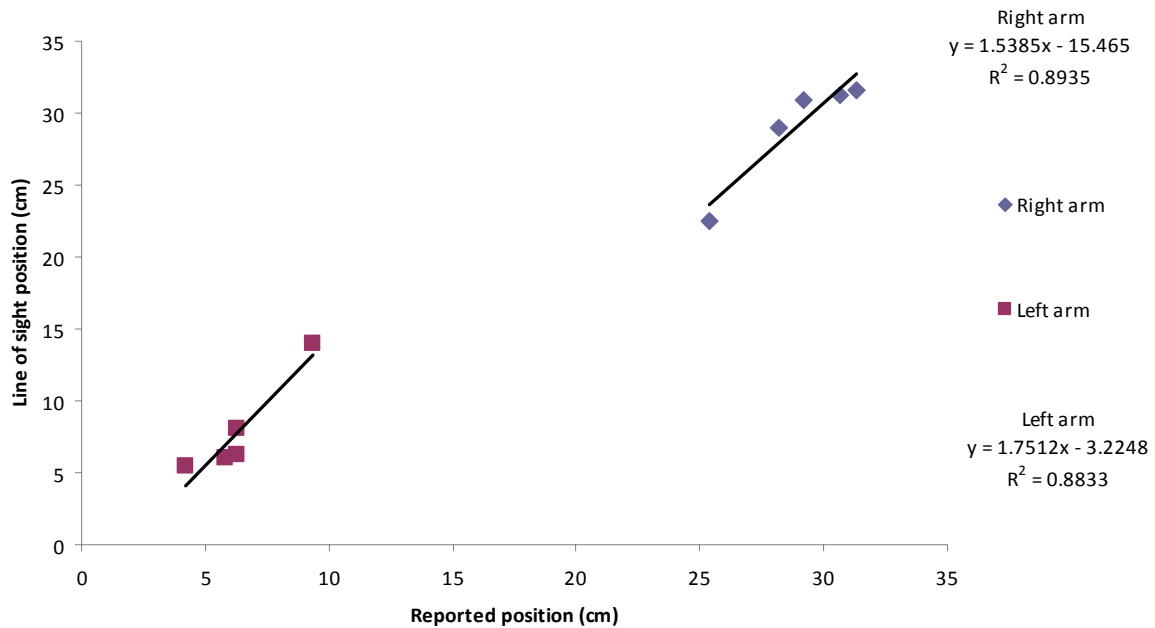


Figure 16: Transformed line of sight and reported positions for the left and right arms (medio-lateral plane)

Summary of results and a comparison of the foreshortening between touched positions

In theory positions closer to the body should have less “foreshortening” in the sagittal plane as shown in figure 13 i.e., L1 should be greater than L2. This directional prediction was confirmed by comparison of constant error. The constant error (difference) between actual and reported distances (actual – reported) for each participant’s mean were compared between the five positions on each arm using a one way repeated measures ANOVA. There was a significant difference between the five positions for the left, $F(4, 60) = 9.239$, $p < .001$ and right arms, $F(2.349, 17.264) = 12.301$, $p < .001$. Post hoc tests revealed there were significant difference between all comparisons except between 20% - 40% and 40% - 60% for the right arm. For the left arm only when comparing 40% - 80% and 60% - 80% were there no significant differences.

A foreshortening effect is present where positions further from the shoulder are reported by the participants as significantly closer to the body than the actual position (Figure 12). This serves to illustrate that positions closer to the body resulted in less foreshortening error in the sagittal plane and that the data follow the logic of a foreshortening effect (Figure 13). Inspection of Figure 12 show that errors as large as approximately eight centimetres are present before correction for foreshortening. Figure 14 shows that the error is reduced to a maximum of approximately 0.7cm for position 0% and a maximum of two cm for all positions on both left and right arms once the adjustment for foreshortening has been made. Indeed, the regression equation in Figure 14 & 16 shows that this is almost proportional, with a very small intercept (1.1cm) for the sagittal plane, and 1.5cm for the medio-lateral plane. A slope of almost exactly 1 (sagittal) and 0.9 (medio-lateral) was also recorded. This possible foreshortening effect will be considered in the discussion. The remainder of the data presented in the results section will always use the *reported* positions between conditions and will not entail comparisons between the actual position and the reported position. Foreshortening is therefore not a factor in these relative positions. .

Sagittal plane analysis

The KFE

To determine if a KFE occurred as described in Craske et.al (1984), two analyses were undertaken. The first used an approach similar to that reported by Craske & Kenny (1984), namely the analysis of changes in perceived position of the button and the probe over trials during active button pressing. The logic of this comparison is that if a KFE is induced in the 12.7cm displaced probe condition, the perceived positions of the button and the probed location should converge over trials. In addition, the current experiment allowed a second approach to determine whether a KFE occurred. If such an effect was in evidence, it would be expected that, on touching the limbs immediately after the 12.7cm displaced probe condition (passive touch condition), participants would report a shift of one or more of the touched limb locations in the sagittal plane. Figure 17 displays the mean perceived position of the button and probe (sagittal plane) over the three blocks during the 12.7cm displaced probe condition.

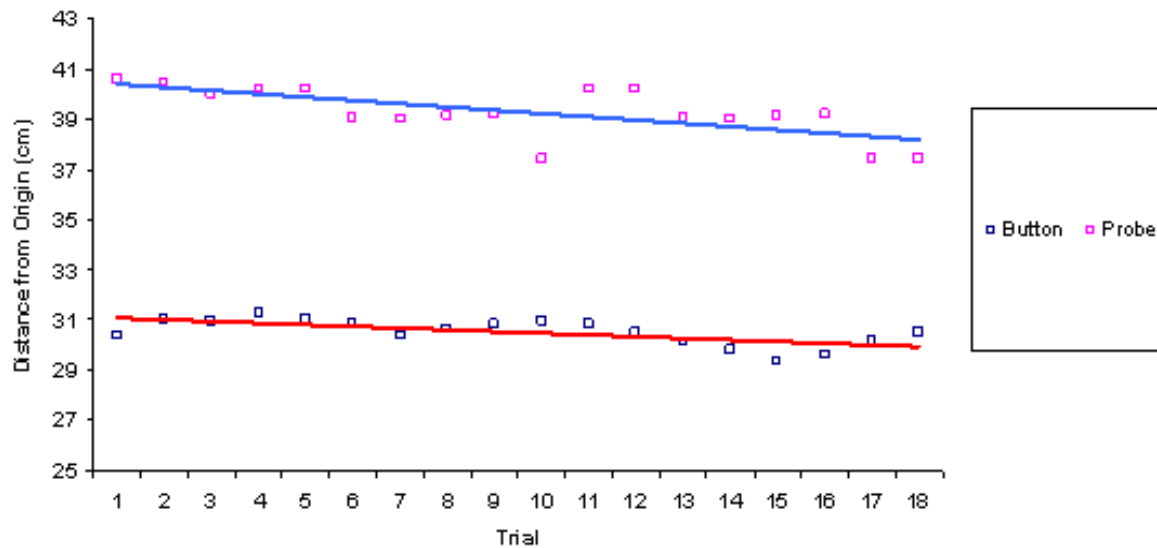


Figure 17: Perceived position of the button and probe during the 12.7cm displaced probe condition

- This graph shows that there was no convergence over trials. One block is made up of six trials. Although the perceived position of the probe was perceived to move gradually slightly closer to the button there was no significant change $F = (2.043, 30.647) 1.511$, $p > 0.05$. On the other hand the button which had been described as moving closer to the probe in the experiments by Craske et.al (1984) slightly moves in the opposite direction away from the probe (closer to the origin) $F = (4.857, 72.862) 1.313$, $p > 0.05$. The two lines would expect to converge if a KFE was present. Overall, there is no KFE as described previously.

- There were no significant differences in the perceived positions between conditions after the passive touch by the examiner for either arm $F(2.627, 39.409) = .959, p = .412$.

Sphericity was not assumed and analysis was undertaken using the Greenhouse-Geisser adjustment. Mean and standard deviations are illustrated in Table 2. The means for this data are also present in Figure 11.

Position	Baseline	After 0cm	After 12.7cm	Baseline	After 0cm	After 12.7cm
	Mean	displacement	displacement	Mean	displacement	displacement
	(right)	Mean (right)	(right)	(left)	Mean (left)	Mean (left)
0%	30.83 (5.57)	29.51 (9.02)	29.51 (8.75)	30.95 (7.10)	30.30 (10.11)	29.86 (8.83)
20%	34.97 (5.39)	34.73 (8.27)	33.92 (8.21)	35.84 (6.16)	35.86 (8.01)	34.62 (8.99)
40%	41.91 (5.11)	40.95 (7.47)	40.47 (8.71)	41.91 (6.05)	41.97 (7.05)	41.48 (7.01)
60%	48.78 (5.4)	48.23 (7.10)	48.23 (8.31)	49.49 (5.15)	48.44 (6.05)	49.73 (6.73)
80%	54.46 (3.55)	54.24 (5.29)	53.06 (6.20)	55.72 (2.45)	53.65 (4.84)	55.03 (4.04)

Table 2: Mean perceived position during passive probed condition for the three conditions for right and left arms. Standard deviation in parentheses

Medio-lateral plane analysis

During the 0cm displaced active button probe condition there was a significant difference between conditions for the left, $t(15) = -5.060, p < 0.001$ and right index finger $F(1.124, 30) =$

8.542, $p < 0.01$ (Figure 18). Both fingers, left (2.35cm) and right (2.40cm) were perceived to be more medial during the active button probe condition.

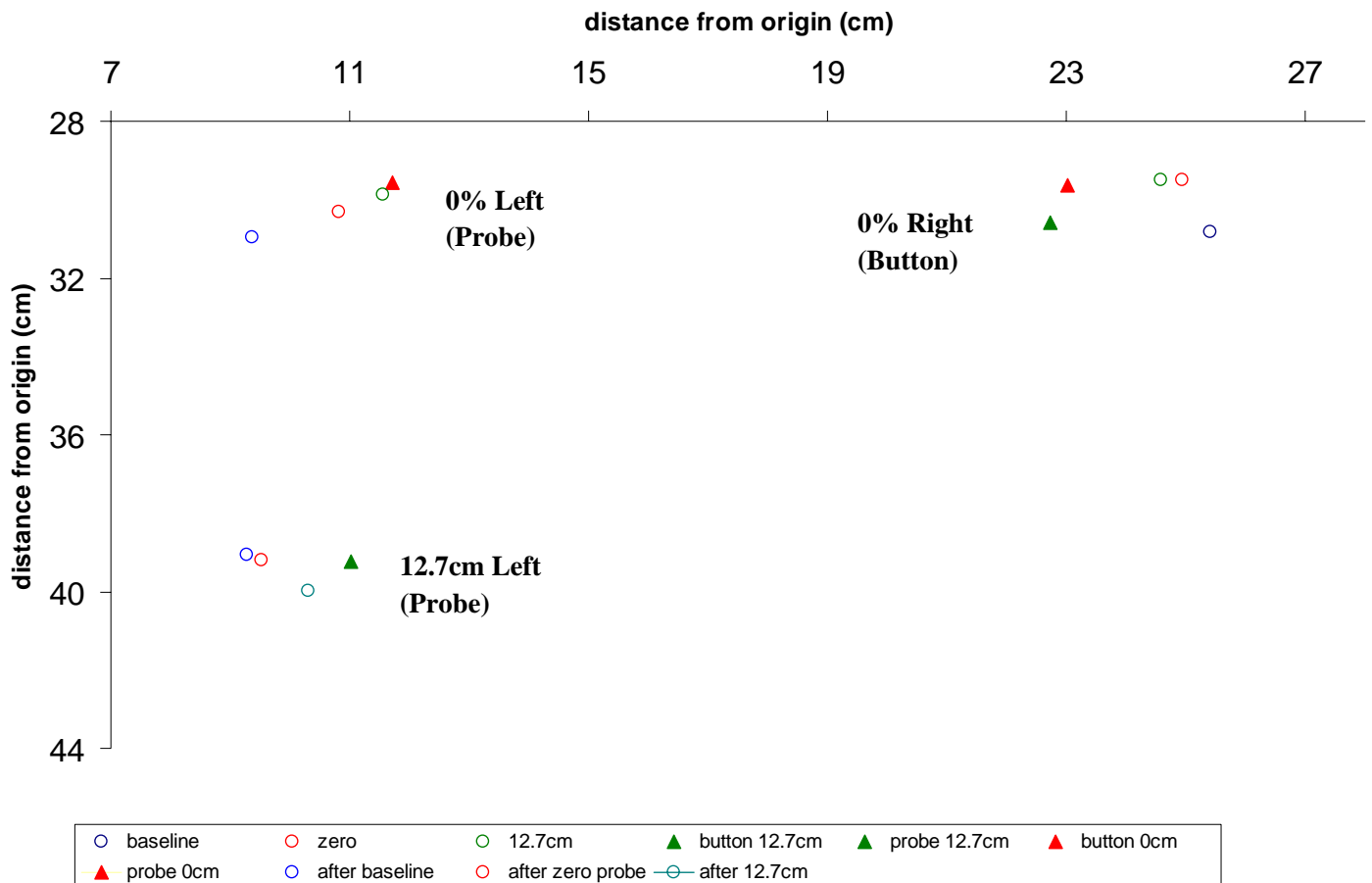


Figure 18: Perceived position for 0% of arm length for the left and right arms and the 12.7cm displaced position for the left arm over the conditions

* Unfilled circles represent passive touch; filled triangles represent perceived position during active button probe condition

After exposure to the 0cm displaced active button probe condition, there was a significant medial shift during the passive probe condition at the left fingertip (2.19cm) $F(4.067, 61.011) = 6.750$, $p < 0.001$; Figure 18). Although the right index finger was perceived as being significantly more medial during the *active* button probe task, in the *passive* probe condition there were no significant differences between the three conditions $F(2.627, 39.309) = .959$, $p > 0.05$; Figure 18).

Two one-way repeated measures ANOVA revealed significant differences between the three conditions in the active button probe task $F(2, 14) = 8.552$, $p < 0.05$) and the passive probe after the 12.7cm displaced probe condition, $F(2, 14) = 7.135$, $p < 0.05$) when comparing the 12.7cm displaced position (Figure 18). The 12.7cm position was perceived as being more medial during (1.75cm) and after (1.03cm) (passive probe by examiner) the active button probe condition.

Perceived separation

Medio-lateral plane

There was a significant decrease in the perceived medio-lateral separation of the right and left index fingers from the baseline when compared to during the 0cm displaced probe condition $F(1.428, 21.420) = 6.914$, $p < 0.01$. The decrease in perceived separation was substantial (approximately 4.75 cm), as shown in (Figure 18). When the perceived medio-lateral separation of the right index finger (0%) and the 12.7cm displaced position in the baseline during the 12.7 displacement condition were compared, a similar significant decrease was observed $F(2, 14) = 17.592$, $p < 0.001$. The decrease in perceived separation was again substantial (approx 4.46 cm), as shown in Figure 18.

Tactile Acuity (baseline)

Sagittal plane

Figure 19 displays the variable error (standard deviation) during the baseline condition for the five positions on left and right arms. The variable error (VE) decreases for both left and right arms for touched positions closer to the body, suggesting that participants had better acuity for positions closer to the body. Post hoc analysis revealed, in general, significantly lower VE at the positions closer to the body $F(4, 60) = 3.565, p < 0.05$ for the left arm during the baseline condition between (Figure 19). There were also significant differences $F(2.254, 60) = 4.316, p < 0.05$ for the VE for the right arm during the baseline condition between 0% - 80%, 20% - 40%, 20-80%, 80% had significantly less VE than all other positions of arm length (Figure 19).

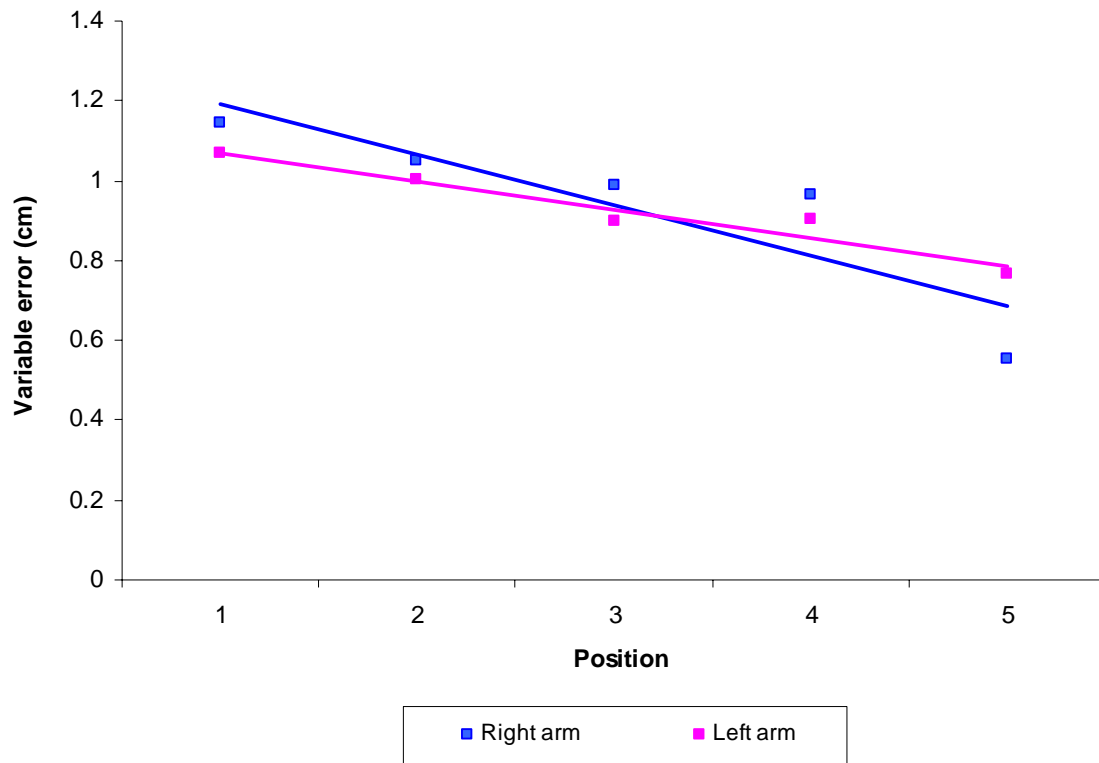


Figure 19: Variable error (mean standard deviation) during the baseline condition for the five positions on left and right arms

*position 1 corresponds to 0% of arm length, 2 as 20% etc.

Medio-lateral plane

There was a clear reduction in VE in the medio-lateral direction for touched positions that were closer to the body. These reductions were significant $F(4, 60) = 2.868, p < 0.05$ for the right arm during the baseline condition between 0% - 60%, 20% - 60%, 40% - 60% and 60% - 80% of arm length (Figure 20). There was also a significant reduction $F(2.254, 60) = 4.316, p < 0.05$ for the left arm during the baseline condition between 0% - 80%, 20% - 40%, 20% - 80%, and 80% had significantly less variable error than all other positions of arm length (Figure 20).

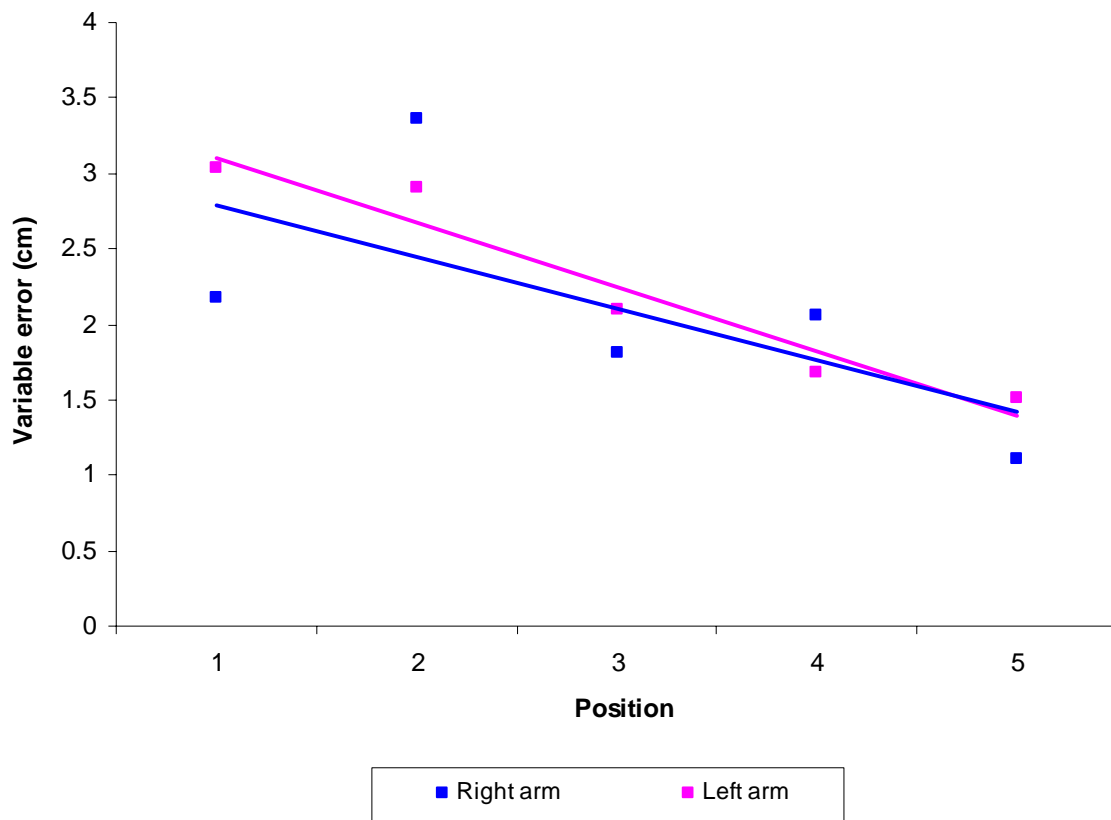


Figure 20: Variable error for left and right arms during the baseline condition*

*position 1 corresponds to 0% of arm length, 2 as 20% etc.

Discussion

The findings presented in the results section will now be considered in light of the existing literature on the KFE as well as on a range of related topics. First, a collection of studies that have identified several precursors for the induction of a perceptual fusion of stimuli will be considered to explain the non replication of the KFE in the sagittal plane and the new finding of a partial fusion in the medio-lateral plane. Second, two possible explanations for the foreshortening of the touched positions, one methodological the other a proposed distance judgement mechanism from the existing literature, will be outlined. Next, an explanation for the finding of localised changes in perceived position will be discussed in light of the existing literature from rubber hand illusion experiments. An alternative account for the short-term perceived medial shift for the right finger will be presented, along with a discussion of the graded acuity for positions on the arm. Future research ideas will be presented in conjunction with some of the key points.

The Kinaesthetic Fusion Effect

There was no replication of KFE as described by Craske et.al (1984) and therefore there was no apparent change in perceived limb length or limb position in the sagittal plane. An explanation for these contradictory findings will now be presented.

Bedford (2004) lists the four possible reactions to a discrepancy between stimuli:

The differing values from the two modalities could indicate that (a) one hand can be in two places at the same time, which would be a fact about the world (“oh wow”); (b) one of the observer’s sense modalities is providing erroneous location information, because the observer knows that what he or she is detecting is not possible (“uh oh”); (c) there are just two different hands, one in each position (“ho hum”); or (d) there is one big hand that extends through both positions, and the observer is detecting a different part through each modality. The second conclusion is required to get an internal perceptual change that involves a shift in seen or felt locations (adaptation).

Bedford (2001), Welch (1972), and Bertelson (1999), have advocated that a ‘unity assumption’ must be met for perceptual change and adaptation. The internal unity assumption is thought to comprise cognitive (top down) and sensory (bottom up) factors and a failure to achieve unity through either of these aspects could have contributed to the non-fusion in the sagittal plane presented in the results of this thesis.

The following three subsections aim to highlight the factors that may have caused the non-fusion in the sagittal plane.

Instructions

Welch (1972) demonstrated that instructions can influence intersensory bias by telling participants in his experiment that the hand they viewed through prisms when pointing at targets was an image of someone else's hand. This resulted in a reduction in adaptation compared to when the participant was not told that the hand did not belong to them. It is possible that there were differences in the instructions provided in this study and in Craske et.al (1984), but after reading the details provided in the method sections of previous publications, no differences could be readily identified.

Familiar association

Bedford (2001) calls the perceptual changes that occur during sensory conflict a 'paradox for perceptual plasticity', where chaos in perception would occur if there was not a internal mechanism that could control the number of possible ways in which the world is perceived to operate. As a result, this model treats events that have not been previously associated together as less likely to be grouped together. Thurlow and Jack (1973) provided an example of this, and found that a whistling kettle with steam induced a strong fusion, whereas lights flashing and bells chiming simultaneously reduced the effect. The unity assumption is also strengthened by increasing the number of shared amodal properties between the conflicting sensory systems.

This internal model that corrects discrepant sensory information and groups familiar events together could be responsible for the non-occurrence of the KFE. The model appeared to have the ability to discriminate between the stimuli; this was, perhaps, because the stimuli had not been previously associated together so the model did not treat the event as united. The

difference between this study and the KFE may lay in the separation between the button and probe. There has not been any report describing the maximum separation of the button and probe that could still induce a KFE. It could be that 12.7cm is at the threshold for maintaining a fusion. Therefore, it is possible that because this is at the threshold the participants treated the event as two separate stimuli rather than one. A future experiment could test the button and probe distance in a graded manner from a smaller to a larger separation in order to clarify the largest separation that still maintains the fusion.

Perceptual repulsion

The results may be interpreted in light of findings and statements presented in Tsakiris et.al (2005). ‘Perceptual repulsion’ was described as occurring during intersensory conflict in a rubber hand illusion experiment. A ruler was positioned so the participants could verbally report a number corresponding to the position of the index finger. Data was collected during a baseline condition and after the participant watched a neutral object being stroked while their unseen finger was simultaneously stroked. There were perceptual shifts in opposite directions – specifically, further from the object when a stick was stroked, and closer when a finger on the rubber hand was stroked. This “perceptual repulsion” was proposed to reveal a behavioural attribute when stimuli are differentiated as either belonging to the individual or as separate from the person. The repulsion may be a necessary process of the internal body representation to distinguish between stimuli that could not possibly be linked even though they share a common temporal binding. The results in this thesis reflect these ideas where not only did the button and probe lack a fusion in the sagittal plane, but there was also evidence of a perceived divergence

between the button and probe. Therefore, it is suggested that the internal model caused a spatial repulsion to differentiate the stimulus provided simultaneously on both arms

Why was a fusion evident in the medio-lateral plane and not the sagittal?

When stimuli have a common spatiotemporal origin, a grouping is more likely to bind them into a single multisensory perceptual object or event (Bedford, 2001). The only observable difference between the two conditions presented in this thesis was that during the 12.7cm displaced probe condition; the stimuli (button and probe) were separated in two dimensions, whereas the 0cm displaced probe was only separated in the medio-lateral plane. Perhaps this was enough for the participants to treat the stimuli as two separate objects or events. The medio-lateral distance between the probe and button was not mentioned in Craske et.al (1984) but may have been smaller. In such a situation, the perceptual system of the participant in that experiment may have only been faced with a spatial discrepancy in the sagittal plane, which was enough for the stimuli to be grouped as one object, and then allowed fusion in the sagittal plane.

For that reason, further experiments are needed to clarify the exact cause of a non-fusion as found in this study. The differences between this study and those presented by Craske et.al (1984) are restricted to just a few factors. The reporting method was changed to allow a more precise measurement of the effect. The non-replication may be attributed to the robust method used here; it could, therefore, be argued that previous methods and measurements were not suitable for the question. For example, an inconsistency in the results presented in Craske et.al (1981) and (1984) highlight this. In Craske. et al, (1981), the participants made reports about the perceived separation of the button and probe by verbally describing the distance in inches. On

the other hand in 1984, a method was introduced which involved judging the button or probe in relation to a light directly above. The 1981 study reported the mean perceived separation after the 12.7cm displaced probe condition to be 2.54cm, whereas in 1984, the reported separation after the 12.7cm displaced probe was of 8.26cm. This demonstrates that their reporting schemes are inconsistent and call into question the robustness of the effect and the adequacy of the reporting method. By comparing the method presented in this thesis with those reported by Craske et.al, 1981, 1984, an indication of the factors that influence the effect can be outlined. Furthermore, if both methods were compared, the results could indicate if the non-replication was due to a change in method or because the effect does not exist in certain contexts, such as elucidating a spatial separation threshold which results in a non fusion. Other factors that could have affected the KFE include the arms resting on foam instead of being held in front by the participant. Visual environmental cues were prevented by a box that surrounded the surface at the table participants sat, and headphones were worn to block auditory cues. Every other element of the experimental procedure was identical or comparable.

The foreshortening effect

The foreshortening effect described in the results caused a systematic shift of the reported touched positions from their actual location to ones closer to the body and more medial. These results support the findings from previous research that behavioural judgements are superior to psychophysical judgements for accurately representing physical qualities of the environment (Sedgwick, 2001; Andre, Rogers, 2006). This explains why previous research (van beers et.al, 1998; Wann et.al, 1992) involving judgements of hand position during visual occlusion have not

found the foreshortening of touched positions, because those studies involved a behavioural method for estimates of position.

This section will present two possible explanations for the results presented in this thesis. The first deals with a methodological explanation involving the method of reporting which could arise when covering the arms with a surface. This will be referred to as the line of sight explanation. The second account involves the possibility of a perceptual distortion due to the lack of perceptual cues required to estimate distance. The necessary literature will be presented to introduce this idea.

1. **The line – of - sight explanation**

After calculation of the projected line of sight position onto the surface between the eyes and the touched position, a near perfect correlation with an intercept close to zero and a slope close to one was found between the reported positions and the position that lie on the line of sight.

Therefore, although the participants were instructed to choose a position directly above the touched position, the majority of individuals chose a position along a line between the estimated eye position and the touched position. This appears to be an artefact of the method used and it is important that any future research using this tool is aware of this possibility. Here it is proposed the participants had a predisposition to choose a position along the line of sight.

2. Perceptual distortion caused by a lack of distance cues

A number of studies have detailed how humans perceive a target's distance. A trigonometric relation links the perceived distance of a target to the angular declination and eye height for the observer from the ground surface, which can be expressed as an equation (Sedgwick, 2001):

$$\text{Distance} = (\text{eye height}) * \tan (\text{angular declination})$$

Ooi, Wu, He (2001) found support for the angular declination contribution to distance estimates in a group of participants judging target distances on the ground surface while wearing base-up prism goggles. The prism distortion caused an increase in the angular declination and the observer significantly underestimated the target distance. An after-effect was also evident causing a subsequent overestimation of target distance, suggesting the nervous system relies heavily on the angular declination to perceive a target's distance. Because the study presented in this thesis involved visual occlusion of the limbs, the participants made distance judgements using tactile and proprioceptive signals only. The results imply that the surface covering the arms caused a distortion for reporting the touched position. Perhaps the visual system's reliance on the angular declination and eye height that could not be utilised may have caused this foreshortening effect.

Typically, the research in distance estimation previously undertaken has involved vision of the target or auditory cues (Ashmead, Davis, Northington, 1995). This study has asked how touch and proprioceptive signals contribute to judging egocentric distance. These results can add to previous findings that the ground surface is used as a reference frame in a process named the sequential surface integration process (SSIP). For example, when vision of the target is allowed

but the ground surface is disrupted by a gap or a variety of textures, underestimates in distance judgements occur. Only when the surface is uniform can accurate judgements be made (Sinai et al, 1998). This study used a novel approach to distort the ground surface reference frame by preventing vision of the surface the target rested on. The study therefore advocated that not only do gaps and texture differences cause distortion in ground reference, but that covering the target with a surface approximately 12cm in height results in misjudgements of distance when relying on the interaction of touch and proprioception. When the ground surface is not available for depth cues, an intrinsic bias of the visual system is treated as the ground surface (Wu, He, and Ooi, 2008). The intrinsic bias causes the visual system to slant the surface or curve upwards, which increases as egocentric distance also increases, thus causing a foreshortening of the target. Wu, He, and Ooi, 2004 state,

“intrinsic bias of the visual system is usually masked in the full-cue light environment, and it exerts little or no influence unless the extrinsic depth cues are inadequate or unavailable for representing surfaces”

The intrinsic bias could possibly explain the results recorded here, as the data follows that found by Ooi, We, He (2005), where although the judged distance was significantly foreshortened, the coding of direction was correct. A compression hypothesis for the underestimation of target distance has previously been identified (Ooi, He, 2007), but does not appear to fit the data presented here, as the compression hypothesis does not accurately maintain the target's direction.

Ooi, He, (2007), explain the compression hypothesis

“The horizontal compression hypothesis states that the horizontal ground is represented as a horizontal surface that is horizontally compressed toward the observer. The perceived target distance on the horizontally represented ground is reduced. Although both hypotheses predict distance underestimation, the horizontal compression hypothesis does not accurately maintain the target’s direction (angular declination).”

Therefore, the results found in this experiment support the slant surface hypothesis in distance estimation when ground surface details are not available. Eye height in relation to the target is used to estimate distance, Sedgwick (1986). Because the surface prevented these cues, it is proposed that the perceptual system was not able to integrate this information to accurately judge distance.

Future research

A future experiment could determine if the intrinsic bias can be reduced or increased when the height of a covering surface is altered. An increase in height may result in an increase in the foreshortening; alternatively, a decrease in the height may result in less foreshortening.

Additionally, there may be a limit to foreshortening at an arbitrary threshold where a top down process results in the person knowing that it is not possible that the distance could be as large or small as the foreshortening suggests. If foreshortening does not significantly differ when comparing different surface heights, this would suggest that the distortion is caused by the intrinsic bias of the visual system and the bias cannot be altered if the target (touched position) remains in the same position. Furthermore, an experiment that allows visual cues of the eye

height and ground surface texture could detail the observed findings. By covering proximal positions of the arm with a clear surface but not the touched fingertip may result in a decrease in the foreshortening effect by allowing eye height and ground surface cues to be integrated into distance judgement. Magnification of proximal body segments may result in misjudgements in eye height. Additionally, if instructions were given that at no time should the individual report a position based on their line of sight, it would allow an evaluation of the hypothesis that an individual can override any predisposition to make judgements based on the line of sight.

The participants in this experiment were surprised by the difference in the expected and actual locations of their arms in relation to the grid once they removed their arms from the apparatus. The verbal reports given by the participants in this study echo those findings of Harrar and Harris (2009) and Gross, Ross and Melzack (1974), who found that covering the arm with a flat surface induced a perceived shortening of the arm only for the participants to say “that they felt that their arm appeared to grow the instant the cover was removed!” Additionally Bastian (2010) calculated subjects’ underestimation of the forearm length and this resulted in an 11.4% decrease in total distance from the elbow to index fingertip. The studies earlier described (Harrar, et.al 2009; Gross, et.al, 1974; Fuentes, et.al, 2010) may need to correct for this foreshortening because their results do not present an explanation for a reported shortening of the limb. Therefore the reported shortening of the limb may not due to any perceptual distortion at all, but rather an artefact of the reporting method.

Touch does not appear to be required, as the results from Gross, et.al, (1974) and Fuentes, et.al, (2010), in which touch was not administered, produced identical findings. If the foreshortening is

caused purely by the method used here and is separate to a perceptual distortion, it is important that future research projects are aware of the distortion that has been described here. It is important for necessary corrections to the data to be undertaken, as well as for theoretical purposes when interpreting data related to the processing of vision, touch and proprioception. The results may also have implications for estimates of distance when vision of the target is not directly available, such as when relying on other sensory systems to provide distance information.

After careful consideration of both explanations for the foreshortening effect, it seems more likely that an artefact of the method used is the most appropriate rationalisation. This is because the line of sight explanations makes fewer assumptions about perceptual processes and shows a high quantitative fit to the data.

Medial shift after active contact

During the active button probe conditions for both 0cm displacement and 12.7cm displacement, the areas touched by the button and probe were perceived as significantly more medial than during the baseline condition. After the active button probe condition and during the passive probe condition, only the positions that had been probed were still perceived as significantly more medial compared to the baseline. The right index finger that pressed the button was not perceived as significantly more medial compared to the baseline during the passive probe condition. An explanation of the grouping of the stimuli in the medio-lateral axis is now presented.

The results of the perceived medial shift during the active button probe condition are not surprising as they correspond to the laws of perceptual grouping (Han, Humpherys, Chen, 1999). The principles of Gestalt grouping – proximity (spatially close objects), similarity (similar elements), and common fate (elements moving simultaneously with the same speed and direction) – are all presented to the perceptual system to organise. This may account for the observed medial shift of the positions on the finger and hand. Additionally, Chang, Nesbitt and Wilkins (2007) have provided evidence that the Gestalt principles of similarity and proximity apply to haptic elements.

The organisation of amodal properties appears to be present from birth. Infants, like adults, are able to organise sensory signals to perceive and group stimuli together (Flom, Bahrick, 2007). Amodal properties such as spatial location, tempo, rhythm, texture and intensity can form the perceptual landscape for an individual. This is illustrated by studies involving infants who are shown to unite audible and visible speech (Lewkowicz, 2000; Walker-Andrews 1997). Flom, Bahrick (2007) highlight the integration of amodal properties:

Temporal synchrony between auditory and visual stimulation, such as the impacts of a bouncing ball, can specify that the two sources of stimulation “go together” and constitute a unitary event.

This process of human perception is important not only for identifying unitary events, but also allows the individual to eliminate stimuli that are not associated with a certain situation. For

example, when a hand from another person moves at the same time as we pick up a glass, we do not perceive the other hand as ours because of the spatial discrepancy.

Bertelson (1999) discusses multimodal grouping in relation to the Ventriloquist Illusion. He suggests that synchronisation between auditory and visual signals is responsible for the fusion of the stimuli, the crossmodal bias and recalibration. The spatial separation between the stimuli is also important for grouping, where an increase in separation results in a loss of fusion (Bertelson & Radeau, 1981). Therefore, it appears that in the medio-lateral plane the spatial separation and synchrony threshold for a loss of fusion was not exceeded, allowing a grouping of the stimuli. Furthermore, this fusion could have been detrimental to the fusion in the sagittal plane, and there may have been a trade off between a fusion in the two axes. If the spatial separation in the medio-lateral direction was close to zero, the perceptual system may allow a fusion in the sagittal plane as reported previously (Craske et.al, 1984)

Cholewiak (1999) was able to demonstrate that the magnitude estimate of two spatially separate touches to the skin was influenced by the interstimulus interval (ISI). A briefer ISI led to a smaller magnitude estimate for a given physical separation. The participants in the experiment of this thesis may have been influenced by the interval when judging the separation of the touches from the button and the probe. Because of the small interval (approximately 100ms) between the pressing of the button and feeling the probe, a bias may be to perceive the stimuli as closer than they actually were. By comparing the ISI at a range of intervals, this hypothesis could be tested. On the other hand this explanation runs counter to the report by Craske et.al, 1981, that a delay of four seconds between the button press and feeling the probe still produced fusion. However,

this finding is especially surprising, as previous sensory conflict experiments have shown that a visual feedback delay of 0.3 seconds for hand movement abolishes the unity assumption (Held & Durlach, 1993). It is not clear at this time, which theory is incorrect and further analysis is required.

Another reasonable suggestion for the cause of the fusion is that of lateral inhibition of touch as described in the ‘funnelling illusion’ which results in a phantom sensation mid-way between the areas that have been touched (von Békésy, 1967). Von Békésy (1967) described funnelling as a characteristic of the nervous system, where sound, vision and touch share the same properties when multiple simultaneous stimulations are presented to the receptors. The simultaneous stimuli were suggested to cause a central core excitation, surrounded by an area of weaker signals. The resultant sensation is dependant on the spatial and temporal overlap, as well as the intensity of the stimuli. Therefore, the cause of the perceived reduction in medio-lateral distance may be the inhibition of the stimuli peripherally to cause a central excitation area. This study provides evidence that the funnelling illusion may occur between the limbs.

Localised changes

The results showed that only the touched positions during the active button probe conditions resulted in a perceived medial shift. This was highlighted by the fact that partial fusion of the touched positions did not extend to nearby landmarks, in particular the closest position (i.e. 20% of limb length). This suggests that the fusion takes place only for the patches of skin that are touched simultaneously and does not cause a perceived shift of the entire limb. These results complement findings from a study of the rubber hand illusion (Tsakiris, et.al, 2005) in which

only those body segments directly involved in the intersensory conflict were affected. Only one finger was stroked for each trial and the rubber hand was stroked on the corresponding finger. The participant was requested to report the location of either the stroked or the un-stroked fingers in relation to a ruler above their unseen hand. The positional changes for the rubber hand illusion were considerably greater for the fingers that were stroked since associations were ascertained for only those fingers, and absent for un-stroked fingers. Therefore, the medio-lateral findings are consistent with existing theories for crossmodal conflict situations. The fusion of the stimuli appears to be the characteristic for perceiving one's own body, while not combining the stimuli may be the trait of actions not related to the person (Tsakiris, et.al, 2005).

Left but not right index finger position perceived to shift medially during passive probe

The fusion found during the active button probe condition did not follow during the passive probing by the examiner on the right index finger, but remains for the left index finger and 12.7cm displaced position. What is different about the right finger and left probed positions in this task? The left limb is entirely passive throughout and receives a light touch by a probe when the right index finger activates a button 12cm to the right. This could explain the variation in the observed results. It may be that the medial shift of the right index finger is only temporary due to its role in the task, whereas the left index finger is shifted for a longer period. A corollary discharge provides a source of limb position during *voluntary* muscle contractions (Sperry, 1969). This discharge acts as a copy of the signal sent to the muscle to areas of the cerebral cortex (Proske, Wise, Gregory, 2000). This discharge is thought to be compared to feedback from the peripheral receptors so corrections can be made to unwanted movements.

Gandevia, Smith, Crawford, Proske and Taylor (2005) found a similar change in the perceived position of the index finger to the results presented here. When the finger was restricted movement but the participant attempted to flex the finger, an illusory position change occurred in the direction of the movement. The perceived medial shift of the right index finger during the active button probe condition may result from the motor command sent from the CNS. However, when the active button probe condition is completed, the motor command has stopped and therefore the perceived medial shift has stopped. Alternatively, the left finger may still be perceived as medial after the active probe condition. This finger did not participate in any motor actions and therefore no default shift has occurred once the condition has concluded. To determine if this is the case, the examiner could activate two probes to contact the index fingers simultaneously. Presuming there is a medial shift from both fingers during this task, this would provide the opportunity to establish if the simultaneous external stimulus caused the permanent medial shift for both fingers, where the medial shift remains during the passive touch task. This would suggest that when a motor command has been executed and causes the perception that the finger has moved in the direction that the force is applied, the CNS treats this as a temporary shift, until the effort subsides. However if the two touches on the index fingers caused by an external stimulus remain during the passive probe it would suggest the CNS does not treat this as a fleeting change in position and updates its internal model long-term.

Tactile/Proprioceptive acuity

There was a significantly larger variable, absolute, and constant error for positions successively further from the body for both left and right arms during the baseline condition. This analysis was undertaken to consider the ability of the participants to localise spatially different touched

positions on the arm during visual occlusion. Variable error increases during a number of different contexts. Foley (1970) found that an increase in variability of verbal estimates of a visual marker increased as a function of the distance from the body. Auditory distance location is especially hard for humans (Yost, 2008), and variability in limb movement distance is a function of target distance (Schmidt, Zelaznik, Hawkins, Frank, Quinn, 1979). In recent times, proprioceptive localisation of the hand has shown the same properties (Wilson, Wong, Gribble, 2010; van Beers, et.al, 1998).

This experiment assessed errors and acuity separately. Errors provide information related to the perceived position of the limb but do not reflect the noise in processing of the tactile or proprioceptive signal where larger variability reveals greater noise in the system. Therefore, the standard deviations of the participants' scores or variable error were used as a measure of acuity. Recently a number of studies have investigated proprioceptive acuity during visual occlusion in different positions of Cartesian space (Wilson, Wong, Gribble, 2010; Van beers, Sittig, Denier Van Der Gon, 1998; Jones, Cressman, Henriques, 2010) after the knowledge that localisation deteriorates during extreme arm postures (Rossetti, Meckler, Prablanc, 1994). The first set of studies in this field of research involved asking the participant to localise their occluded fingertip by pointing at it with the contralateral limb. Research that is more recent has introduced localisation over the workspace by indicating the position of their hand and finger in relation to a proprioceptive reference or a visual reference on the surface covering the arms (Wong, et.al, 2010). This change in methodology was in response to the concern that reaching and pointing to the perceived location of a body part was not a true measure of proprioceptive acuity alone, as the addition of motor output to the task could introduce kinematic errors (Jones, et.al, 2010).

These ideas can be coupled with those of Dijkerman and de Haan (2007), who propose that proprioception for perception and action are processed separately, and therefore pointing at a position will not reveal the perception of the participant. This project continued this line of exploration by asking participants to localise a touched position in relation to a grid above their arms and thereby eliminating any errors caused by motor output. In comparison to these new methodologies, the original contribution from the experiment presented in this document involved quantifying participants' estimates of a position in space by mapping *tactile* signals onto *proprioceptive* signals, not only at the *fingertip* and *hand* but at positions on the *forearm*. This enquiry has not been undertaken formerly, where *proprioceptive* acuity has only been concerned with the hands or finger (Jones et.al, 2010; Fuentes, Bastian, 2010; Wilson, et.al, 2010) or elbow angle (Fuentes, Bastian, 2010). The results here are consistent with those studies that were concerned only with proprioceptive acuity of the hand or finger. Specifically, Van Beers et.al (1998) and Wilson, et.al, (2010) both found that hand positions closer to the shoulder are localised better than positions further away, although this was not found for joint proprioception (Fuentes, et.al, 2010). Here, touched positions further from the torso on both the left and right upper limbs were localised with significantly more absolute error and a significantly larger variable error than those closer to the body in both the sagittal and medio-lateral planes. These findings and those by other authors (Wilson, et.al, 2010; van Beers et.al, 1998) suggest that proprioception alone and touch and proprioception in combination are localised with greater acuity for positions closer to the body, but joint angles do not use the same reference frame (Fuentes, et.al, 2010).

Furthermore, these findings are in contrast to research that has shown that positions that are more distal have a higher density of receptors and therefore a lower two-point threshold compared to more proximal body segments (Stevens, Choo, 1996). This demonstrates that receptor density has no influence on spatial localisation. This is not surprising, since receptor density would in theory provide superior localisation only in relative judgements confined to the region of skin involved, and has no bearing on spatial judgements made in a larger, egocentric reference frame. In this case, spatial localisation is superior for positions closer to the body, and implies no relation to receptor density; coding has occurred within a different reference frame. Therefore that receptor density (and hence acuity) would only influence tasks such as two-point discrimination (i.e. relative judgments in the region of skin involved), but give no better information about their position in space.

The cause of this uncertainty in acuity for more distal positions has been explained by a similar study involving localisation of the hand position for different elbow angles (van Beers, et.al, 1998). The authors suggested that the larger inaccuracies for localising the hand during a position of elbow extension compared to flexion were associated with the shape and size of the ellipse that represented the distribution of localisation. In an extended arm the noise in the signal about the angle of the shoulder and elbow occur in the same direction, resulting in a stretched ellipse compared to that of the flexed elbow position. The flexed elbow position has noise effects in different directions and results in a smaller ellipse. The distance between the shoulder and hand is also smaller in this situation, resulting in less noise for the shoulder angle position. These principles have been used to explain the superior acuity for localising the hand when the hand is closer to the body, and the results of this thesis support this. The brain codes for the position of

the body and the surrounding environment in extrinsic (visually based) and intrinsic (joint based) coordinates (Newport, Rabb, Jackson, 2002). Transfer and generalisation after adaptation to force field perturbations is coded in an intrinsic coordinate system as inter-limb transfer is observed (Shadmehr and Moussavi, 2000). Generalisation after adaptation to visuomotor rotation is coded in extrinsic coordinates (Krakauer, Ghilardi, Ghez, 1999). An experiment could be designed to determine the coding of touch, by asking participants to estimate touched positions with the elbow extended to 180 degrees or flexed at 90 degrees. If the touch is coded in extrinsic coordinates, acuity should not change when the elbow is flexed or extended, because there is no visual information with which to compare the position, while acuity may change when the joint angle changes and codes for an intrinsic coordinate system.

Conclusions

In summary, when the arms are visually occluded, simultaneous touched positions on each arm led to a localised partial medio-lateral, but not a sagittal plane fusion of the stimuli, as had been previously detailed (Craske et.al, 1984). Tactile acuity was found to decrease progressively for distal positions of the upper limb. In addition, a foreshortening effect was found which may result from a line-of-sight judgment resulting from the reporting method used.

Future research should focus on further clarification of the ‘unity assumption’, i.e., the conditions that must be present for a fusion effect to occur. Delineating these requirements (e.g. spatial proximity, particularly the separate and combined effects of the medio-lateral and sagittal plane separation of the limbs) could help to explain why the KFE may occur in some conditions but not in others.

All studies of the perceived locations of the unseen limbs necessarily require the selection of an appropriate reporting method. The current study used a method that, while improving on that used in the original report of the KFE by using a two-dimensional visual reference system, introduced a specific distortion (foreshortening). Future studies to compare alternative location reporting methods would also benefit this field of study. In particular, a specific evaluation of the ‘line-of-sight’ hypothesis might enable the validation of mathematical corrections to remove the observed distortions.

References

- Aglioti, S, DeSouza, J.F.X, Goodale, M.A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology*, 5, (6), 679-85.
- Allen, T.J, Proske, U. (2006) Effect of muscle fatigue on the sense of limb position and movement. *Experimental Brain Research*, 170, (1), 30-38
- Alles, D.S. (1970) Information transmission by phantom sensations. *IEEE Transactions on Man-Machine Systems*, 11, (4), 85 -91
- Allison, G, Fukushima, S. (2003) Estimating three-dimensional spinal repositioning error: the impact of range, posture, and number of trials. *Spine*. 29, 2510 –2516
- Andre, J, Rogers, S. (2006) Using verbal and blind-walking distance estimates to investigate the two visual systems hypothesis. *Perception and Psychophysics*, 68, 353–361.
- Armel, K.C, Ramachandran, V.S. (2003) Projecting sensations to external objects: evidence from skin conductance response. *Proceedings of the Royal Society, Biological Sciences*, 270, 1499-1506
- Ashmead, D.H, Davis, D.L, Northington, A. (1995). Contribution of listeners' approaching motion to auditory distance perception. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 239–256.

Bastian, A.J. (2008) Understanding sensorimotor adaptation and learning for rehabilitation. *Current opinion in neurology*, 21, (6), 1350-1355

Bays, P.M, Wolpert, D.M. (2007) Computational principles of sensorimotor control that minimize uncertainty and variability. *The Journal of Physiology*, 578, (2), 387–396

Bedford, F. L. (2001). Towards a general law of numerical/object identity. *Cognitive/Current Psychology of Cognition*, 20, 113-175

Bedford, F. L. (2004). Analysis of a Constraint on Perception, Cognition, and Development: One Object, One Place, One Time. *Journal of Experimental Psychology: Human Perception and Performance*, 30, (5), 907–91

Bernier, P.M, Burle, B, Vidal, F, Hasbroucq, T, Blouin, J (2009) Direct evidence for cortical suppression of somatosensory afferents during visuomotor adaptation. *Cerebral Cortex*, 19, (9), 2106-2113

Bertelson, P, Radeau, M. (1981). Cross-modal bias and perceptual fusion with auditory-visual spatial discordance. *Perception & Psychophysics*, 29, (6), 578-84.

Bertelson, P. (1999). Chapter 14 Ventriloquism: A case of crossmodal perceptual grouping. *Advances in Psychology: Cognitive Contributions to the Perception of Spatial and Temporal Events*, 129, 347-362

Bianchil, I, Savardi, U, Bertamini, M (2008) Estimation and representation of head size (people overestimate the size of their head – evidence starting from the 15th century), *British Journal of Psychology*, 99, 513–53

Bodegård, A, Geyer, S, Herath, P, Grefkes, C, Zilles, K, Roland, P.E. (2003). Somatosensory areas engaged during discrimination of steady pressure, spring strength, and kinaesthesia. *Human Brain Mapping*, 20, (2), 103–115

Botvinick, M, Cohen, J. (1998) Rubber hands' feel' touch that eyes see. *Nature*, 391, 756

Boyle, J, Negus, V. (1998). Joint position sense in the recurrently sprained ankle. *Australian Journal of Physiotherapy*, 44, (3), 159-163.

Bremmer, F, Schlack, A, Duhamel, J. R, Graf, W, Fink, G.R. (2001). Space coding in primate posterior parietal cortex. *Neuroimage*, 14(1), 46–51.

Callaghan, M.J, Selfe, J, Bagley, P.J, Oldham, J.A. (2002) The Effects of Patellar Taping on Knee Joint Proprioception. *Journal of Athletic Training*, 37, (1), 19–24

Carpenter, J.E, Blasier, R.B, Pellizzon, G.G. (1998) The Effects of Muscle Fatigue on Shoulder Joint Position Sense. *The American Journal of Sports Medicine*, 26, (2), 262-265

Carello, C, Turvey, M. T. (2000) Rotational Invariants and Dynamic Touch, in M. A. Heller (ed.), *Touch, Representation, and Blindness*, Oxford University Press, New York, NY, USA

Cha, J, Rahal, L, Saddik, A.E. (2008) A pilot study on simulating continuous sensation with two vibrating motors. *HAVE 2008 – IEEE International Workshop on Haptic Audio Visual Environments and their Applications*

Chang, D, Nesbitt, K.V, Wilkins,K. (2007) The gestalt principles of similarity and proximity apply to both the haptic and visual grouping of elements. In *Proceedings of the Eight Australasian Conference on User interface*

Cholewiak, R.W (1999) The perception of tactile distance: influences of body site, space, and time. *Perception*, 28, 851–875

Chu, J.C, Kane, E.J, Arnold, B.L, Gansneder, B.M. (2002) The Effect of a Neoprene Shoulder Stabilizer on Active Joint-Reposition Sense in Subjects With Stable and Unstable Shoulders. *Athletic Training*, 37, (2), 141–145

Clark, F.J, Burgess, P.R. (1975). Slowly adapting receptors in cat knee joint: can they signal joint angle? *Journal of Neurophysiology*, 38, 1448-1463.

Clark, F.J, Larwood, K.J, Davis, M.E, Deffenbacher, K.A. (1995). A metric for assessing acuity in positioning joints and limbs. *Experimental Brain Resesarch*, 107, 73–79

Cohen, J. (1988) *Statistical power for the behavioral sciences*. Erlbaum; Hillsdale, NJ

Cole, J. D. (1991) *Pride and a daily marathon*. London: Duckworth

Connolly, B.H, Montgomery, P. (2004) *Therapeutic Exercise in Developmental Disabilities*: 3rd edition. Slack Incorporated

Costantini, M, Haggard, P. (2007) The rubber hand illusion: Sensitivity and reference frame for body ownership. *Consciousness and Cognition*, 16, (2), 229-240

Craske, B, Kenny, F.T, Keith, D. (1984). Modifying an Underlying Component of Perceived Arm Length: Adaptation of Tactile Location Induced by Spatial Discordance. *Journal of Experimental Psychology: Human Perception and Performance*. 10, (2), 307-317

Craske, B, Kenny, F.T. (1981). The kinaesthetic fusion effect: Perceptual elimination of spatial discordance in the kinaesthetic modality. *Perception and Psychophysics*. 30, (3), 211-216

De vignemont, F, Ehrsson, H.H, Haggard, P. (2005) Bodily illusions modulate tactile perception. *Current Biology*, 15, 1286–1290.

Dijkerman, C, de Haan Edward H. F. (2007). Somatosensory processing subserving perception and action: Dissociations, interactions, and integration. *Behavioral and Brain Sciences*. 30, 224-230

Duchaine, B, Cosmides, L, Tooby, J. (2001). Evolutionary psychology and the brain. *Current Opinion in Neurobiology*. 11, 225–230

Edin, B.B, Johansson, N. (1995). Skin strain patterns provide kinaesthetic information to the human central nervous system. *Journal of Physiology*. 487, 243-251

Ehrsson, H.H, Holmes, N.P, Passingham, R.E. (2005). Touching a Rubber Hand: Feeling of Body Ownership Is Associated with Activity in Multisensory Brain Areas. *The Journal of Neuroscience*, 25(45), 10564-10573

Ehrsson, H.H, Kito, T, Sadato, N, Passingham, R.E, Naito, E (2005) Neural substrate of body size: illusory feeling of shrinking of the waist. *The Public Library of Science: Biology*, 3, 412

Ferrell, W.R, Craske, B. (1992) Contribution of joint and muscle afferents to position sense at the human proximal interphalangeal joint. *Experimental Physiology*, 77, 331-342.

Flom, R, Bahrick, L.E. (2007) The development of infant discrimination of affect in multimodal and unimodal stimulation: The role of intersensory redundancy. *Developmental Psychology*, 43, 238–252

Foley, J.M. (1970). Loci of perceived, equi-, half- and double-distance in stereoscopic vision. *Vision Research*, 10, 1201-1209.

Fuentes, C.T, Bastian, A.J. (2010) Where Is Your Arm? Variations in Proprioception Across Space and Tasks. *Journal of Neurophysiology*, 103, 164-171

Gallagher, S. (2005) *How the Body Shapes the Mind*. Oxford University Press, USA

Gandevia, S.C, Smith, J.L, Crawford, M, Proske, U, Taylor, J.L. (2006) Motor commands contribute to human position sense. *The Journal of Physiology*, 571, 703-710.

Gauthier G. M. , Vercher, J. L. Mussa Ivaldi, F. Marchetti. E. (1988). Oculo-manual tracking of visual targets: control learning, coordination control and coordination model. *Experimental Brain Research*. 73, (1), 127-137

Gandolfo, F, Mussa-Ivaldi, F.A, Bizzi. E. (1996). Motor learning by field approximation. *Proceedings of the National Academy of Sciences, Neurobiology*. (93). 3843-3846

Geisler, W. S, Kersten, D. (2002). Illusions, perception, and Bayes. *Nature Neuroscience*, 5, 508–510.

Gescheider, G.A. (1997) *Psychophysics. The Fundamentals.*, Mahwah, NJ: Lawrence Erlbaum Associates

Goldstein, E, Humphreys, G, Shiffrar, M (2005). Blackwell handbook of sensation and perception. Blackwell Publising

Goodale, M.A, Pelisson, D.P, Prablanc, C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement, *Nature*. 320, 748–750.

Goodale, M.A, Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in neurosciences*. 15, (1), 20-25

Graziano, M.S.A, Cooke, D.F, Taylor, C.S.R (2000) Coding the location of the arm by sight. *Science*, 290, 1782-1786

Gross, Y, Webb, R, Melzack, R. (1974) Central and peripheral contributions to localization of body parts: Evidence for a central body schema. *Experimental Neurology*, 44, 3, 346-362

Gross, Y, Melzack, R. (1978) Body image: Dissociation of real and perceived limbs by pressure-cuff ischemia. *Experimental Neurology*, 61, 3, 680-688

Han, S, Humphreys, G.W, Chen, L. (1999) Uniform connectedness and classical Gestalt principles of perceptual grouping. *Perception & Psychophysics*, 61, 661–674

Harrar, V, Harris, L.R (2009) Eye position affects the perceived location of touch. *Experimental Brain Research*, 198, 403–410

He, Z, Wu, B, Ooi, T, Yarbrough, G, Wu, J (2004) Judging egocentric distance on the ground: Occlusion and surface integration. *Perception*, 33, 789-806

Head, H, Holmes, G. (1911–1912) Sensory disturbances from cerebral lesions. *Brain*, 34, 102–254.

Held, R, Durlach, N. (1993). Telepresence, time delay and adaptation. In S.R. Ellis, M.K. Kaiser, & A.C. Grunwald (Eds.) *Pictorial communication in virtual and real Environments*. London: Taylor and Francis.

von Helmholtz, H. E. F. (1926). Treatise on physiological optics. *Nature*. 118, 74-76.

Jeannerod, M. (1989) The neural and behavioural organisation of goal directed movements. Clarendon Press, Oxford

Jones, L. A. (1988). Motor illusions: What do they reveal about proprioception? *Psychological Bulletin*, 103, 72-86

Jones, S, Cressman, E, Henriques, D (2010) Proprioceptive localization of the left and right hands. *Experimental Brain Research*, 204, (3), 373-383

Kammers, M.P, Kootker, J.A, Hogendoorn, H, Dijkerman, H.C. (2009). How many motoric body representations can we grasp? *Experimental Brain Research*. 202, (1), 203-212

Kammers, M.P., Van Der Ham, I.J., Dijkerman, H.C. (2006). Dissociating body representations in healthy individuals: Differential effects of a kinaesthetic illusion on perception and action. *Neuropsychologia*. 44, (12), 2430-2436

Kaplan, F.S, Nixon, J.E, Reitz, M (1985) Age related changes in proprioception and sensation of joint position. *Acta Orthopédica Scandinavica*, 56, 72–74

Kavounoudias, A , Roll, J.P, Anton, J.L, Nazarian, B, Roth, M, Roll, R. (2008). Proprio-tactile integration for kinesthetic perception: An fMRI study. *Neuropsychologia*. 46, 2, 567-575

Kellman, P, Spelke, E. (1983). Perception of partly occluded objects in infancy. *Cognitive Psychology*, 15, 483-524.

Kelso, J. (1995) *Dynamic patterns: The self-organization of brain and behaviour*. MIT Press, Cambridge.

Kennett, S, Taylor-Clarke, M, Haggard, P (2001) Noninformative vision improves the spatial resolution of touch in humans. *Current Biology*, 11, 1188–119

Kephart, N. C. (1960) *The slow learner in the classroom*. Columbus, Ohio: Merrill

Knox, J.J, Hodges, P.W (2005) Changes in head and neck position affect elbow joint position sense. *Experimental Brain Research*, 165, 107–113

Koralewicz, L.M, Engh, G.A (2000) Comparison of proprioception in arthritic and age-matched normal knees. *Journal of Bone and Joint Surgery*. 82, 1582-1588.

Krakauer, J.W, Ghilardi, M.F, Ghez, C. (1999) Independent learning of internal models for kinematic and dynamic control of reaching. *Nature Neuroscience*. 2, 1026–1031

Lackner, J, DiZio, P (2002) Proprioceptive adaptation and aftereffects. In: Stanney, K. Handbook of Virtual Environments. New York: Lawrence Erlbaum Associates

Lang, C.E, Bastian, A.J (1999) Cerebellar Subjects Show Impaired Adaptation of Anticipatory EMG During Catching, *Journal of Neurophysiology*, 82, 2108-2119

Lephart, S.M, Giraldo, J.L, Borsa, P.A, Fu, H.E. (1996) Knee joint proprioception: A comparison between female intercollegiate gymnasts and controls. *Knee Surgery, Sports Traumatology, Arthroscopy*, 4, (2), 121-124

Lewkowicz, D.J. (1999) Chapter 16 The development of temporal and spatial intermodal perception. *Advances in Psychology: Cognitive Contributions to the Perception of Spatial and Temporal Events*, 129, 395-420

- Lewkowicz, D.J (2000) Infants' perception of the audible, visible and bimodal attributes of multimodal syllables, *Child Development*, 71, (5), 1241–1257
- Longo, M.R, Haggard, P (2010) An implicit body representation underlying human position sense. *Proceedings of the National Academy of Science*, 107, (26), 11727-11732
- Martin, T.A, Keating, J.G, Goodkin, H.P, Bastian, A.J, Thach, W.T. (1996) Throwing while looking through prisms II. Specificity and storage of multiple gaze - throw calibrations, *Brain*, 119, (4), 1199-1211.
- McCall, G.E, Goulet, C, Boorman, G.I, Roy, R.R, Edgerton, V.R. (2003) Flexor bias of joint position in humans during spaceflight. *Experimental Brain Research*, 152, 1, 87-94
- McCloskey, D.I. (1978). Kinesthetic sensibility. *Physiological Reviews*. 58, (4), 763-820
- McDonnell, P.M, Scott, R.N, Dickison, J, Theriault, R.A, Wood, B (1989) Do artificial limbs become part of the user? New evidence. *Journal of Rehabilitation Research and Development*, 26, 2, 17–24
- Meng, J.C, Sedgwick, H.A (2001) Distance perception mediated through nested contact relations among surfaces, *Perception & Psychophysics*, 63, 1-15
- Mizukami, Y, Uchida, K, Sawada, H (2007) Transmission of Stroking Sensation on a Skin by Higher-psychological Perception, *SICE Annual Conference*

Newport, R, Rabb, B, Jackson, S.R. (2002) Noninformative vision improves haptic spatial perception. *Current Biology*, 12, 1661–64.

O’Callaghan, C, Nudds, M (2009) *Sounds and Perception: New Philosophical Essays*, Oxford University Press

Olson, I.R, Gatenby, J.C, Gore, J.C. (2002). A comparison of bound and unbound audio–visual information processing in the human cerebral cortex. *Cognitive Brain Research*, 14(1), 129–138.

Oohara, J, Kato, H, Hashimoto, Y, Kajimoto, H (2010) Presentation of Positional Information by Heat Phantom Sensation. *Haptics: Generating and Perceiving Tangible Sensations. Lecture Notes in Computer Science*, 6192, 445–450

Ooi, T.L, Wu, B, He, Z.J (2001) Distance determined by the angular declination below the Horizon, *Nature*

Ooi, T.L, Wu, B, He, Z.J. (2006). Perceptual space in the dark affected by the intrinsic bias of the visual system. *Perception*, 35, 605–624

Ooi, T.L, He, Z (2007) A Distance Judgment Function Based on Space Perception Mechanisms: Revisiting Gilinsky’s (1951) Equation. *Psychological Review*, 114, (2), 441–454

Pagano, C.C, Turvey, M.T. (1998). Eigenvectors of the inertia tensor and perceiving the orientation of limbs and objects. *Journal of Applied Biomechanics*, 14, 331–359

Paillard, J, Brouchon, M (1968) Active and passive movements in the calibration of position sense. In: Freedman, S.J, *The neuropsychology of spatially oriented behavior*, Dorsey Press, Homewood III.

Paillard, J, Michel, F, Stelmach, G. (1983) Localization Without Content: A Tactile Analogue of 'Blind Sight'. *Archives of Neurology*. 40, (9), 548-551

Paillard, J (1999) Dissociated contribution of movement and position cues in visuo-motor control
In : Gantchev, N, Gantchev, G.N. From Basic Motor Control to Functional Recovery. Academic Publishing House "Pro.M. Drinov", Sofia. Conference on Motor Control 1999, St. Constantine, Varna, Bulgaria

Penfield, W (1950) The Cerebral Cortex of Man: A Clinical Study of Localization of Function. *The Journal of the American Medical Association*, 144, (16), 1412

Pons, T.P, Garraghty, P.E, Ommaya, A.K, Kaas, J.H, Taub, E, Mishkin, M. (1991). Massive Cortical Reorganization After Sensory Deafferentation in Adult Macaques. *Science*. 252, 5014, 1857-1860.

Pratt, J, Abrams, R.A. (1996). Practice and component submovements: the role of feedback in rapid aimed limb movements. *Journal of Motor Behavior*. (28) 149–156.

Proske, U, Wise, A.K, Gregory, J.E (2000) The role of muscle receptors in the detection of movements. *Progress in Neurobiology*, 60, 85–96

Ramachandran, V.S, Hirstein, W, Rogers-Ramachandran, D. (1998) Phantom limbs, body image, and neural plasticity. *International Brain Research*, 26, 10–11.

Ramsay, J, Riddoch, M. (2001) Position-matching in the upper limb: professional ballet dancers perform with outstanding accuracy. *Clinical Rehabilitation*, 15, (3), 324-330

Reitman, E, Cleveland, S (1964) Changes in body image following sensory deprivation in schizophrenic and control groups. *Journal of Abnormal and Social Psychology*, 68, (2), 168-176

Rossetti, Y, Meckler, C, Prablanc, C (1994) Is there an optimal arm posture? Deterioration of finger localization precision and comfort sensation in extreme arm-joint postures. *Experimental Brain Research*, 99, 131-136

Rossetti, Y, Rode, G, Boisson, D. (1995). Implicit processing of somaesthetic information: a dissociation between where and how? *Neuroreport*. 6, (3), 506-10.

Rymer, W.Z, D'Almeida, A (1980) Joint position sense: The effects of muscle contraction. *Brain*, 103, 1-22

Sanes, J.N, Donoghue, J.P. (2000). Plasticity and Primary Motor Cortex. *Annual Reviews in Neuroscience*, 23, 393–415

Schmidt, R.A, Zelaznik, H, Hawkins, B, Frank, J.S, Quinn, J.T (1979) Motor-output variability: a theory for the accuracy of rapid motor acts. *Psychological Review*, 86, 415–451

Schmidt, R.A, Lee, T.D. (1995) Motor Control and Learning: A Behavioral Emphasis. Fourth Edition. Human Kinetics

Sedgwick, H.A. (1986). Space perception. In Boff, K, Kaufman, L, Thomas, J (Eds.), *Handbook of perception and human performance*. New York: Wiley.

Shadmehr, R, Moussavi, Z.M. (2000) Spatial generalization from learning dynamics of reaching movements. *Journal of Neuroscience*, 20, 7807-7815

Shepherd, G.M. (1994). Neurobiology, New York: Oxford University Press

Sinai, M.J, Ooi, T.L, He, Z.J (1998) Terrain influences the accurate judgement of distance. *Nature*, 395, 497-500

Spence, C, Sanabria, D, Soto-Faraco, S. (2007). Intersensory Gestalten and crossmodal scene perception. In: Noguchi, K (ed) *Psychology of beauty and Kansei: new horizons of Gestalt perception*. Fuzanbo International, Tokyo, 519–579

Sperry, R.W. (1969). An emergent theory of consciousness. *Psychological Review*, 76, 532-536.

Stevens, J.C, Choo, K.K. (1996). Spatial acuity of the body surface over the life span.

Somatosensory & Motor Research, 13, 153–166.

Stein, B.E, Meredith, M (1993) *The Merging of the Senses*. The MIT Press

Stillman, B.C (2002) Making Sense of Proprioception: The meaning of proprioception,

kinaesthesia and related terms. *Physiotherapy*, 88, (11), 667-676

Tanaka, H, Worringham, C, Kerr, G (2009). Contributions of vision-proprioception interactions to the estimation of time-varying hand and target location. *Experimental Brain Research*. 195, 371-382

Thomas, J.R, Nelson, J.K. (1990) *Research Methods in Physical Activity* (2nd ed.). Champaign, IL: Human Kinetics

Thurlow, W.R, Jack, C.E. (1973) Certain determinants of the "ventriloquism effect". *Perceptual Motor Skills*, 36, (3), 1171-84.

Tsakiris, M, Haggard, P (2005) The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception and Performance*, 31, 80-91

van Beers, R.J, Sittig, A, van der Gon, J (1998) The precision of proprioceptive position sense. *Experimental Brain Research*, 122, (4), 367-377

van Beers, R.J, Haggard, P, Wolpert, D (2004) The Role of Execution Noise in Movement Variability. *Journal of Neurophysiology*, 91, 1050-1063

Von Békésy, 1967 *Sensory Inhibition* Princeton, NJ: Princeton University Press

Wada, Y, Kitagawa, N, Noguchi, K (2003) Audio–visual integration in temporal perception. *International Journal of Psychophysiology*, 50, (1-2), 117-124

Walker-Andrews, A.S. (1997). Infants' perception of expressive behaviors: Differentiation of multimodal information. *Psychological Bulletin*, 121, 437–456

Walsh, L.D, Smith, J.L, Gandevia, S.C, Taylor, J.L (2009) The combined effect of muscle contraction history and motor commands on human position sense. *Experimental Brain Research*, 195, 603–610

Wann, J. P, Ibrahim, S.F. (1992). Does limb proprioception drift? *Experimental Brain Research*, 91, 162–166.

Welch, R. B. (1972) The effect of experienced limb identity upon adaptation to simulated displacement of the visual field. *Perception and Psychophysics*, 12, 453–456

Welch, R, Warren, D (1980) Immediate Perceptual Response to Intersensory Discrepancy *Psychological Bulletin*, 88, (3), 638-667

Welch, R (1999) Chapter 15 Meaning, attention, and the “unity assumption” in the intersensory bias of spatial and temporal perceptions. *Advances in Psychology: Cognitive Contributions to the Perception of Spatial and Temporal Events*, 129, 371-387

Wilson, E, Wong, J, Gribble, P (2010) Mapping Proprioception across a 2D Horizontal Workspace, *Public Library of Science One*, 5, (9)

Wolpert, D.M, Goodbody, S.J, Husain, M. (1998). Maintaining internal representations: the role of the human superior parietal lobe. *Nature Neuroscience*. 1, 6

Wu, B, Ooi, T.L, He, Z.J (2004) Perceiving distance accurately by a directional process of integrating ground information. *Nature*, 428, 73-77

Wu, J, He, Z, (2008) Perceived relative distance on the ground affected by the selection of depth information. *Perception & Psychophysics*, 70, 707-713.

Zia, S, Cody, F, O'Boyle, D (2000) Joint position sense is impaired by Parkinson's disease. *Annals of Neurology*, 47, (2), 218–228

Appendix 1: Ethics Approval

Dear Dr Charles Worringham

Project Title:

The Kinaesthetic Fusion Effect: mechanisms and extensions

Approval Number: 1000000557

Clearance Until: 15/07/2013

Ethics Category: Human

This email is to advise that your application has been reviewed by the Chair, University Human Research Ethics Committee, and confirmed as meeting the requirements of the National Statement on Ethical Conduct in Human Research.

Whilst the data collection of your project has received ethical clearance, the decision to commence and authority to commence may be dependant on factors beyond the remit of the ethics review process. For example, your research may need ethics clearance from other organisations or permissions from other organisations to access staff. Therefore the proposed data collection should not commence until you have satisfied these requirements.

If you require a formal approval certificate, please respond via reply email and one will be issued.

Decisions related to low risk ethical review are subject to ratification at the next available Committee meeting. You will only be contacted again in relation to this matter if the Committee raises any additional questions or concerns.

This project has been awarded ethical clearance until 15/07/2013 and a progress report must be submitted for an active ethical clearance at least once every twelve months. Researchers who fail to submit an appropriate progress report may have their ethical clearance revoked and/or the ethical clearances of other projects suspended. When your project has been completed please advise us by email at your earliest convenience.

For variations, please complete and submit an online variation form:

<http://www.research.qut.edu.au/ethics/forms/hum/var/variation.jsp>

Please do not hesitate to contact the unit if you have any queries.

Regards


Janette Lamb on behalf of the Chair UHREC
Research Ethics Unit | Office of Research
Level 4 | 88 Musk Avenue | Kelvin Grove
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e: ethicscontact@qut.edu.au

w: <http://www.research.qut.edu.au/ethics/>

Appendix 2:

Participant recruitment flyer

 Queensland University of Technology Brisbane Australia	<h1 style="text-align: center;">PARTICIPATE IN RESEARCH</h1> <h2 style="text-align: center;">Information for Prospective Participants</h2>	
<p><i>The following research activity has been reviewed via QUT arrangements for the conduct of research involving human participation. If you choose to participate, you will be provided with more detailed participant information, including who you can contact if you have any concerns.</i></p>		
<h3 style="text-align: center;">The “Kinaesthetic Fusion Effect”: Mechanisms and Extensions</h3>		
<h4 style="text-align: center;">Research Team Contacts</h4>		
<p style="text-align: center;"> Matt Gildersleeve School of Human Movement Studies 0424238759 m.gildersleeve@qut.edu.au </p>	<p style="text-align: center;"> Dr Charles Worringham – Supervisor School of Human Movement Studies 3138 6172 c.worringham@qut.edu.au </p>	
<p style="text-align: center;">Please contact the research team members to have any questions answered or if you require further information about the project.</p>		
<h4>What is the purpose of the research?</h4>		
<p>The purpose of this research is to understand interaction between the senses of touch and limb position.</p>		
<h4>Are you looking for people like me?</h4>		
<p>The research team is looking for male and female QUT Undergraduate or Postgraduate students between the ages of 18 and 30. We invite anyone with normal or corrected vision and with no injuries to the arm and hands to take part.</p>		
<h4>What will you ask me to do?</h4>		
<p>Your participation will involve one session of about an hour at the Institute of Health and Biomedical Innovation (IHBI). During the experiment you will be seated with your arms outstretched on a table in front, underneath a surface to hide your limbs. On each of a set of trials, you will be asked to press a button. A probe will be felt on the opposite limb, after every time the button is pressed you will be asked a question about where you feel the probe. One experiment will involve pointing without vision of both limbs to a single visual target.</p>		
<h4>Are there any risks for me in taking part?</h4>		
<p>There are no risks beyond normal day-to-day living associated with your participation in this project, though it is possible that you could feel minor discomfort from maintaining a fixed arm position for short periods. Frequent rest breaks will be offered, and you can request additional rest breaks at any time.</p> <p>If you do agree to participate, you can withdraw from participation at any time during the project without comment or penalty.</p>		
<h4>Are there any benefits for me in taking part?</h4>		
<p>It is expected that this project will not directly benefit you. However, it may lead to a better understanding of how humans plan limb movements by investigating sensory interaction of touch and limb position sense.</p>		
<h4>I am interested – what should I do next?</h4>		
<p>If you would like to participate in this study, please contact the research team (contact details are given above). You will be provided with further information to ensure that your decision and consent to participate is fully informed.</p>		
<h2 style="text-align: center;">Thank You!</h2>		RM Reference Number: 1000000557

Appendix 3: Participant consent form



PARTICIPANT INFORMATION for QUT RESEARCH PROJECT

The “Kinaesthetic Fusion Effect”: Mechanisms and Extensions

Research Team Contacts

Matt Gildersleeve	Dr Charles Worringham – Senior Lecturer
School of Human Movement Studies	School of Human Movement Studies
0424238759	3138 6172
m.gildersleeve@qut.edu.au	c.worringham@qut.edu.au

Description

The purpose of this project is to understand the interaction of touch and limb position sense. The research team requests your assistance to participate in an experiment on this topic if you are between the ages of 18 or 40, have normal or corrected vision and have no injuries to the arms or hands

Participation

Your participation in this project is voluntary. If you do agree to participate, you can withdraw from participation at any time during the project without comment or penalty. Your decision to participate will in no way impact upon your current or future relationship with QUT (for example your grades) or with the researchers involved.

Your participation will involve resting your arms on a surface and pressing a button. A probe will be felt on the opposite limb, after every time the button is pressed you will be asked a question about where you feel the probe. One experiment will involve pointing without vision of both limbs to a single visual target, without using vision. . Experiments will take place at the Institute of Health and Biomedical Innovation (IHBI), and will take approximately 60 minutes for the participant involvement.

Expected benefits

It is expected that this project will not directly benefit you. However, it may lead to a better understanding of how

humans plan limb movements by investigating sensory interaction of touch and limb position sense.

Risks

There are no risks beyond normal day-to-day living associated with your participation in this project, though it is possible that you could feel minor discomfort from maintaining a fixed arm position for short periods. Frequent rest breaks will be offered, and you can request additional rest breaks at any time.

Confidentiality

All comments and responses are anonymous and will be treated confidentially. The names of individual persons are not required in any of the responses.

Consent to Participate

We would like to ask you to sign a written consent form (enclosed) to confirm your agreement to participate.

Questions / further information about the project

Please contact the researcher team members named above to have any questions answered or if you require further information about the project.

Concerns / complaints regarding the conduct of the project

QUT is committed to researcher integrity and the ethical conduct of research projects. However, if you do have any concerns or complaints about the ethical conduct of the project you may contact the QUT Research Ethics Officer on +61 7 3138 5123 or email ethicscontact@qut.edu.au. The Research Ethics Officer is not connected with the research project and can facilitate a resolution to your concern in an impartial manner.

Thank you for helping with this research project. Please keep this sheet for your information.



CONSENT FORM for QUT RESEARCH PROJECT

The “Kinesthetic Fusion Effect”: Mechanisms and Extensions

Research Team Contacts

Matt Gildersleeve	Dr Charles Worringham – Senior Lecturer
School of Human Movement Studies	School of Human Movement Studies
0424238759	3138 6172
m.gildersleeve@qut.edu.au	c.worringham@qut.edu.au

Statement of Consent

By signing below, you are indicating that you:

1. have read and understood the information document regarding this project
2. have had any questions answered to your satisfaction
3. understand that if you have any additional questions you can contact the research team
4. understand that you are free to withdraw at any time, without comment or penalty
5. understand that you can contact the Research Ethics Officer on +61 7 3138 5123 or ethicscontact@qut.edu.au if you have concerns about the ethical conduct of the project
6. agree to participate in the project

Name

Signature

Date

/

/

The following form is optional – you may choose to include it with materials for participants, or delete the page if not using.



WITHDRAWAL OF CONSENT FORM FOR QUT RESEARCH PROJECT

The “Kinesthetic Fusion Effect”: Mechanisms and Extensions

Research Team Contacts

Matt Gildersleeve	Dr Charles Worringham – Senior Lecturer
School of Human Movement Studies	School of Human Movement Studies
0424238759	3138 6172
m.gildersleeve@qut.edu.au	c.worringham@qut.edu.au

I hereby wish to WITHDRAW my consent to participate in the research project named above.

I understand that this withdrawal WILL NOT jeopardise my relationship with Queensland University of Technology.

Name

Signature

Date

/

/
